CONDITIONAL STRATEGIES IN THE INTRASPECIFIC INTERACTIONS OF SALTICID SPIDERS: WHY FIGHT?

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Abstract

Salticid spiders have exceptionally intricate display behaviour during interactions between conspecific individuals. That courtship (male-female display) is related to intersexual selection appears to be well established, but the function of intrasexual display remains poorly understood. My objective was to clarify the external variables that influence the decision rules of salticids during intrasexual interactions. Three species of salticids were tested: *Euophrys parvula* from New Zealand, and *Jacksonoides queenslandicus* and *Portia fimbriata* from Australia. Intrasexual conflict was observed between pairs of salticids in the presence and absence of optical or olfactory cues from potential resources (mate and prey). When displays escalated more often in the presence of a resource, compared with the absence of these cues, it was viewed as competition for the resource. Movement alone, in the absence of other cues, does escalate competitions between male *E. parvula* and is an important control in determining the value of resources. Although male salticids escalated intrasexual competitions in the presence of visual and/or olfactory cues from conspecific females, female salticids did not escalate competitions in the presence of cues from conspecific males. However, female, but not male *P. fimbriata* did escalate intrasexual interactions in the presence of olfactory cues from a common prey species, *J. queenslandicus*. These results support predictions from sexual selection theory that females are a valuable resource to males and that intrasexual selection may have shaped the decision rules used during male-male competition in salticids.

Chapter 1: Introduction

Sexual selection is a special subset of natural selection proposed by Darwin as a way to explain the evolution of secondary sexual characteristics, complex courtship and intrasexual conflict behaviour. Traditionally, two categories of sexual selection are recognised: intersexual selection, which is a consequence of mate choice behaviour and intrasexual selection, which is a consequence of competition between individuals of one sex for mating opportunities. Intersexual selection tends to be more often primarily a consequence of females choosing particular kinds of males instead of vice versa. Intrasexual selection is more often primarily a consequence of male-male instead of female-female conflict. However, there are important exceptions to both of these trends.

One group of animals that exhibit pronounced male-male conflict are spiders from the family Salticidae. With nearly 5,000 described species (Coddington & Levi 1991; Zabka 1993), the salticids are the largest family of spiders. In contrast to most spiders, the salticids have very acute vision with resolution abilities that have no known parallels in other animals of comparable size (Land 1969a,b; Blest et al. 1990; Jackson & Harland 1998; Harland et al. 1999). Most salticids are diurnal, cursorial predators of arthropods, mainly insects, and employ vision to guide prey capture sequences (Forster 1982a; Jackson & Pollard 1996; Harland & Jackson 2000).

It is probably not surprising that vision also plays a large part in the intraspecific communication of salticid spiders. These displays comprise various postures of the body, palps and legs (Jackson 1982a), and have been the subject of study for over a century starting with the Peckhams (1889,1890). The Peckhams studied both male-male aggressive displays in addition to displays associated with courtship.

Since the Peckhams initial work, salticid display has been studied extensively (Crane 1949; Jackson 1982a; Richman & Jackson 1992). The main emphasis of these studies has been on courtship displays. Salticid courtship tends to be an intricate behaviour actively performed by the male, with the apparent aim of persuading the female to mate with the male. While saying that intersexual selection explains the evolution of courtship displays would be overly simplistic, there is at least limited evidence that females choose males with which to mate on the basis of male display (Jackson 1982b; Jackson & Pollard 1997).

The relationship between salticid male-male display and intrasexual selection is, in contrast, more of a puzzle. The problem is partly the absence of clear evidence that salticid male-male interactions fit any of the better-known patterns associated with intrasexual selection in other animals, such as social dominance, resource-based territoriality or leks (Andersson 1994). Instead, what is established is more limited.

1) When salticid males meet, they tend to display and often progress to contact behaviours in which one participant may be injured or even killed (and eaten).

2) Similar female-female interactions may occur, but in most salticids studied female-female interactions are less intense (shorter in duration, less often progressing to contact behaviour and less often resulting in injury or death).

3) The display behaviour of salticid males (and females) is different depending on whether the partner is the same or opposite sex. In intraspecific interactions, for example, the salticid often extends its fangs, spread its forelegs to the side and raises its body. In contrast, salticids tend to keep their fangs retracted, legs extended forward and bodies lowered during intersexual interactions.

To date, no satisfactory hypothesis can explain the ultimate cause behind these dangerous male-male displays. Salticid male-male display behaviour has the appearance of conflict over a resource. It has become common to argue, or presume, that the resource is mating opportunities. However, more evidence is needed to judge whether this conclusion is justified.

Game theory has become an important tool for studying animal conflict (Maynard Smith & Price 1973; Maynard Smith 1982). As in optimality theory (Stephens & Krebs 1986), game theory depends on cost-benefit ratios, where the costs and benefits should relate to fitness. However, game theory differs from more traditional optimality models by incorporating a consideration of the contingencies arising from interactions in which each animal is subject to different cost-benefit variables of its own.

Three predictions from game theory have been especially influential (Maynard Smith & Parker 1976, Parker & Rubenstein 1981);

1) The cost the contestant is willing to incur by fighting (contest cost) increases with increasing resource value.

2) When contestants have different fighting ability (also often called "resource holding potential" or "RHP": Parker 1974) and these abilities can be perceived by the contestants, this asymmetry is used by the contestants to settle the outcome of contests more quickly than would otherwise happen. In particular, size is often a good predictor of RHP, and it is predicted that when there is a pronounced size discrepancy the contest will end especially quickly, with the larger individual winning. Note that this is not the same as saying something simpler and probably more obvious: that the larger individual will tend to win fights.

3) The willingness of contestants to accept greater cost increases when perceived RHP (e.g., perceived size) becomes more similar.

Contests are often characterised by two parameters: duration and intensity. Intensity refers to the rate at which cost accumulates when the animal adopts a behaviour. For example, the contact behaviour of salticids during male-male interactions would appear to be high intensity because being in contact must put the salticid in harm's way more so than displays performed at a distance.

Salticid male-male interactions have been studied recently in relation to game-theory prediction 2 & 3 (Jackson & Cooper 1991; Faber & Baylis 1993), but there has been only one study (Wells 1988) that has also investigated prediction 1. Prediction 1, however, is potentially the most important in solving the mystery of why salticid males interact aggressively.

Wells (1988) studied a New Zealand salticid, *Euophrys parvula*, in which display behaviour is especially intricate (Jackson & Willey 1995). In experiments, males were allowed to interact both in the presence and in the absence of a conspecific female. There were no complications in these experiments deriving from the female also interacting with the males because the females used were "lures" made from dead, dried conspecific females mounted on a cork. Using lures instead of live females is feasible in studies of salticids because of the remarkable acuity of salticid eyes. We know that salticids can distinguish on the basis of optical cues alone, and in the absence of movement, conspecifics from typical prey, the sex of the conspecific, the species of prey, and many other details of the animal it sees (Jackson & Tarsitano 1993; Jackson 1995; Harland & Jackson 2000).

Wells (1988) found no relationship between the contest duration and the presence of the lure but he found that males escalated the intensity of interactions more when in the presence of a lure than when not. This finding is of special interest because it would appear to support the hypothesis that male-male display is related to intrasexual selection. However, testing this hypothesis was not explicitly Wells' objective. Instead, his objective was to test whether game theory could explain the structure of salticid interactions. He assumed that females were the relevant resource. Testing this assumption was not his goal.

Additional research is needed in order to test the intrasexual-selection hypothesis. What we know is that *E. parvula* males alter their display behaviour during male-male interactions depending on whether a conspecific female is present or not. We do not know how specific this finding is: is it specifically the presence of a conspecific

female that influences the males' decisions? Answering this question will require controls that were absent from Wells' (1988) study.

My objective was to extend the work of Wells (1988). Instead of testing game theory predictions as such, my goal was to examine in detail the influence of outside stimuli (i.e., stimuli coming from sources other than the two interacting individuals) on the decisions salticids make when interacting with conspecifics of the same sex.

As an outside stimulus, Wells (1988) used only the optical cues coming from a lure made from a dead conspecific female. I extended this work by substituting other cues and by investigating female-female, as well as, male-male interaction. I used both optical cues and chemical cues, and initially there were two alternative working hypotheses.

In this thesis, I investigate the hypothesis that conditional strategies govern intrasexual conflict behaviour in salticids. A conditional strategy can be thought of as a set of decision rules that govern the intrasexual conflict behaviour. These decision rules dictate which alternate behaviour, hereafter called tactics, a male should employ during a given conflict (see Dominey 1984). Terms like 'strategy' and 'tactics' when used colloquially imply a degree of cognition. For example, the Concise Oxford dictionary (1999) describes a 'tactic' as "an action or strategy carefully planned to achieve a specific end". However, in biology no cognitive functions need be attributed to these decision rules (i.e., the decision rules (if any) employed by salticids are not consciously acted on).

In conditional strategy terms, the decision rule that seems to be operating can be stated: escalate male-male conflict if a conspecific female is present. If this rule applies then it has implications on sexual selection. Intrasexual selection seems to apply to these salticids, a fact that has been assumed until now but has not been tested scientifically. Studying the rules governing conditional strategies can be envisaged as asking an animal, in experiments, what resources matter to it.

Three species of salticids are used in this study: *Euophrys parvula*, *Portia fimbriata*, and *Jacksonoides queenslandicus*.

1) ***Euophrys parvula.***

This spider is found throughout the North Island and in the South Island as far south as Christchurch (Forster & Forster 1999), where they are commonly seen sunning them selves on the side of houses. *E. parvula* is of particular importance because it is the species on which Wells (1988) based his study.

This New Zealand salticid is sexually dichromatic; females are almost uniformly brown, while males have black legs and a red patch on the top of the cephalothorax. The stylised postures used by *E. parvula* during both intrasexual and intersexual interactions have been well studied (Jackson and Wiley, 1995, Wells, 1988). Interestingly, *E. parvula* employ the third pair of legs during display that is an uncommon occurrence as most spiders display using the first pair of legs (Forster & Forster 1999).

2) ***Portia fimbriata.***

P. fimbriata is important because it uses chemical cues (Pollard et al. 1987, Willey & Jackson 1993) and is araneophagic (Jackson & Wilcox 1998). *P. fimbriata* is unusual because, besides hunting prey cursorily, the species in the genus build prey-catching webs and also hunt in the webs of other spiders. *P. fimbriata*'s preferred prey are other spiders (Li and Jackson, 1996; Li et al., 1998) that are captured after web invasion and the use of aggressive-mimicry signals (Jackson & Wilcox 1998).

In this genus of 15-20 species from Africa, Asia and Australia, the predatory strategy of Queensland *P. fimbriata* is unique because it includes a specialised style of stalking (called "cryptic stalking") used specifically for capture of other species of salticids. Both the males and the females of Queensland *P. fimbriata* prey on salticids, but neither sex adopts cryptic stalking against conspecifics. Queensland *P. fimbriata* females stalk salticids larger

than themselves, but males prey only on smaller salticids (Li & Jackson 1996).

Recent studies (Clark et al, in press; Jackson et al, in prep) have suggested that the tactics employed by Queensland *P. fimbriata* for capturing salticids is a by-product of tactics developed to capture the salticid *Jacksonoides queenslandicus*. *J. queenslandicus* is the most common salticid that coexists with Queensland *P. fimbriata* in the rainforests of Queensland, Australia (Jackson 1988). The Queensland population of *P. fimbriata* have evolved behaviours that aid in the location (Jackson et al in prep) and capture (Clark et al in press) of *J. queenslandicus.* Chemical cues from *J. queenslandicus,* from draglines or olfactory cues (kairomones) trigger these behaviours. If the predatory strategies of Queensland *P. fimbriata* for dealing with salticids are a consequence of tactics first developed for hunting *J. queenslandicus,* this implies that *J. queenslandicus* must be a valuable resource for these *Portia*. If *J. queenslandicus* are such a valuable resource then escalation should be detected during intrasexual conflicts, possibly even in male-male conflict, even though males generally have a lesser interest in food compared with females.

3) ***Jacksonoides queenslandicus.***

Jacksonoides queenslandicus comes from Queensland, Australia, and is sympatric with *Portia fimbriata*. As is typical of most salticids, *J. queenslandicus* is a cursorial predator that hunts by day retreating to silken nests at night (Jackson 1988). *J. queenslandicus* preys on a mixture of spiders and insects using visual guided sequences, as is typical of jumping spiders (see Forster 1982) as a means of catching prey rather than by building a web. Silk production is limited to draglines and the silk tube that it spins for a nest.

Jacksonoides queenslandicus is the most common species that *P. fimbriata* preys upon in Queensland. Recent studies (Clark et al, in press) have shown that Queensland *P. fimbriata* respond in a predatory fashion to inadvertently released olfactory cues (kairomones) from this particular prey species.

Chapter 2: Optical cues that influence male-male conflict in *Euophrys parvula*, a New Zealand jumping spider.

INTRODUCTION

Sexual selection is a special subset of natural selection proposed by Darwin (1859) as a way to explain the evolution of secondary sexual characteristics, complex courtship and intrasexual conflict behaviour (Andersson 1994). Traditionally, two categories of sexual selection are recognised: intersexual selection, which is a consequence of mate choice behaviour, and intrasexual selection, which is a consequence of competition between individuals of one sex for mating opportunities with the opposite sex (Krebs & Davies 1993; Ryan 1997). Although there are important exceptions to both of these trends, intersexual selection tends more often to be primarily a consequence of females choosing particular kinds of males instead of vice versa and intrasexual selection more often is primarily a consequence of male-male instead of female-female conflict.

Early on, jumping spiders (Salticidae) were important in the literature on sexual selection. In particular, during the 19th century, the Peckhams (1889,1890), who were strong supporters of Darwin's theory of sexual selection, studied the courtship (intersexual display) and male-male (aggressive display) behaviour of North American salticids.

Salticidae, with nearly 5,000 described species (Coddington & Levi 1991; Zabka 1993), are the largest family of spiders. Most species of salticids are cursorial, diurnal predators and all have excellent eyesight (Jackson & Pollard 1996). Although spider eyes generally lack the structural complexity required for acute vision (Homann 1971; Blest 1985), salticids have unique, complex eyes with resolution abilities that have no known parallels in other animals of comparable size (Land 1969a,b; Blest et al. 1990; Jackson & Harland 1998; Harland et al. 1999). Highly developed vision may make studying sexual selection especially tractable in salticids.

Salticid courtship, which was studied extensively in the century following the Peckhams' initial work (Crane 1949; Richman 1982; Jackson 1982a; Richman & Jackson 1992), tends to be an intricate behaviour actively performed by the male. Salticid females tend to be less active at displaying during intersexual encounters, their primary objective appearing to be to decide, on the basis of male display, whether to mate. Although the advantage gained by salticid females when exercising choice is not well understood, there is at least limited evidence that females do actually choose the particular males with which to mate (Jackson 1982b; Jackson & Pollard 1997). Intersexual selection appears to go a long way in explaining the evolution of male courtship display behaviour.

The relationship between salticid male-male display and intrasexual selection is, in contrast, more of a puzzle. The problem is partly the absence of clear evidence that salticid male-male interactions fit any of the better-known patterns associated with intrasexual selection in other animals, such as social dominance, resource-based territoriality and leks (Andersson 1994). Instead, what has been established is more limited (see Jackson & Pollard 1997);

1) When salticid males meet, they tend to display and often progress to contact behaviour in which one participant may be injured or even killed (and eaten).

2) Similar female-female interaction may occur. However, in most of the salticids that have been studied, female-female interaction appears to be less intense (i.e., female-female interaction tends to be shorter in duration, less often progressing to contact behaviour and less often resulting in injury or death).

3) The display behaviour of salticid males (and females) differs depending on whether

the partner belongs to the same or the opposite sex. In intraspecific interactions, for example, salticids often extend their fangs, spread their forelegs to the side and raise their bodies, whereas salticids in intersexual interactions tend to keep their fangs retracted, legs extended forward and bodies lowered. Intrasexual display makes sense as a mechanism for revealing to another salticid that the displaying individual is dangerous (i.e., it makes sense to call the behaviour observed " threat behaviour"), whereas the opposite appears to be the case for the male's display behaviour during intersexual encounters (courtship).

All spiders are predators, primarily of other arthropods (Foelix 1996). Salticids tend to take prey comparable to themselves in size, and cannibalism is a fact of life for these spiders (Richman & Jackson 1992). Defence against cannibalism is probably relevant generally when salticids interact, and this factor has probably had a role in shaping some of the details concerning how salticids interact, including the exceptional complexity and flexibility of salticid display (Jackson & Pollard 1997). However, early attempts (Savory 1928; Bristowe 1941) to explain the function of salticid courtship as being mechanisms by which the male identifies himself to the female as a conspecific male instead of a routine prey (e.g., an insect) do no hold up (Jackson 1982a). Nor do early attempts (Savory 1928) to explain salticid male-male display as mistaken identity (male mistaking another male for a female) hold up. The most telling evidence against the mistaken-identity hypotheses is perhaps the fact that males almost always use different displays from the beginning depending on whether the other salticid is a male or a female (Jackson & Pollard 1997).

That male-male display can be explained simply as anti-predator defence, where the predator in this instance is a conspecific of the same sex, also appears unlikely. In spiders in general, and in salticids in particular, the female tends to take larger prey and feed more often than males (Foelix 1996). More specifically, in salticids, females may often take prey as large or larger than themselves, whereas males tend to take prey smaller than themselves (Enders 1975; Givens 1978; Li & Jackson 1996). Yet it is male-male, not female-female, display that tends to be especially pronounced in salticids, the opposite of what anti-predator defence might predict. Also, salticids tend to flee from typical predators. In contrast, salticid males seem to go out of their way to be noticed when they encounter conspecifics of the same sex. They display, come together and interact actively, after which one male flees (the "loser") and one male holds its ground (the "winner"). Phrased this way, the puzzle is what do the losers lose, and what do the winners win?

Salticid male-male display behaviour has the appearance of conflict over a resource, and it has become common to argue, or presume, that the limiting resource for which males compete are mating opportunities. However, more evidence is needed before we can judge whether this conclusion is justified. One way of seeking this evidence is to apply game theory.

Game theory has become an important tool for studying animal conflict (Maynard Smith & Price 1973; Maynard Smith 1982). As in optimality theory (Stephens & Krebs 1986), game theory depends on cost-benefit ratios, where the costs and benefits should relate to fitness. However, game theory differs from more traditional optimality models by incorporating a consideration of the contingencies arising from interactions in which each animal is subject to different cost-benefit variables of its own (Parker 1974).

Three predictions from game theory have been especially influential (Maynard Smith & Parker 1976, Parker & Rubenstein 1981);

1) The cost a contestant is willing to incur by fighting (contest cost) increases when the value of the resource at stake increases.

2) When contestants have different fighting ability (also often called "resource holding potential" or "RHP": Parker 1974) and these differences in ability can be perceived by the contestants, this asymmetry is used by the contestants to settle the outcome of contests more quickly than would otherwise happen (individual with lesser RHP backs down). There is considerable evidence that size is an especially good predictor of RHP (e.g. Riechert 1982), and often this prediction can be re-stated: when there is a pronounced size discrepancy, the contest will end especially quickly and the larger individual will win. Note that this is not the same as saying something simpler and probably more obvious: that the larger individual will tend to win fights. Instead, what is predicted is that the contestants avoid having serious fights because they quickly ascertain what the probable outcome would be.

3) The willingness of a contestant to accept greater cost increases when a contestant perceives its rival's RHP (e.g., size) to be more similar to its own.

Contests are often characterised by two parameters: duration and intensity. Intensity refers to the rate at which cost accumulates when the animal adopts a stated behaviour. For example, contact behaviour is common in salticids during male-male interactions and this behaviour would appear to be of high intensity (being in contact must put the salticid in harm's way, more so than when displays are performed at a distance).

Salticid male-male interactions have been studied recently in relation to the second and third (see above) game-theory prediction (Jackson & Cooper 1991; Faber & Baylis 1993), but there has been only one study (Wells 1988) that has also investigated prediction 1. Yet prediction 1 appears to be the most important for resolving why salticid males interact aggressively.

Wells (1988) studied a New Zealand salticid, *Euophrys parvula*, in which display behaviour is especially intricate (Jackson & Willey 1995). In experiments, males were allowed to interact both in the presence and in the absence of a conspecific female. There were no complications in these experiments deriving from the female also interacting with the males because the female used was a "lure" made from a dead, dried conspecific female mounted on a cork. Using a lure instead of a live female is feasible in studies of salticids because of the remarkable acuity of salticid eyes, and we know that salticids can distinguish on the basis of optical cues alone, and in the absence of movement, conspecifics from typical prey, the sex of the conspecific, the species of prey, and many other details of the animal it sees (review: Harland & Jackson 2000).

Wells (1988) found no relationship between interaction duration and the presence of a lure, but he did find that the intensity of male-male interaction escalated further when in the presence of a lure and less when not. This finding is of special interest because it would appear to support the hypothesis that the evolution of male-male display has been driven by intrasexual selection. However, testing this hypothesis was not explicitly Wells' objective. Instead, his objective was to test whether game theory could explain the structure of salticid interactions. For this, instead of testing the hypothesis explicitly, he assumed that females were a resource for which males competed.

Testing the intrasexual-selection hypothesis itself requires additional research. What we know is that *E. parvula* males alter their display behaviour during male-male interactions depending on whether or not a conspecific female is present. We do not know how specific this finding is: is it the presence of, specifically, a conspecific female that influences the males' decisions? Answering this question requires controls that were absent from Wells' (1988) study.

Here, instead of testing game theory predictions as such, my goal is to examine in more detail how the decisions *E. parvula* salticid males make when interacting with conspecifics of the same sex are influenced by

outside optical stimuli, where 'outside' means coming from sources other than the two interacting individuals.

Two alternative hypotheses are considered. The first is called the 'general-agitation hypothesis': escalation is entirely a consequence of more or less any extraneous stimulation that puts *E. parvula* males in a state of heightened excitation (general agitation). If this hypothesis holds, then the escalation Wells (1988) documented would appear to be explained as something like an artefact. The second hypothesis ('represents-female hypothesis') is in a more straightforward way compatible with escalation being a consequence of the salticid males making game-theory decisions after perceiving the presence specifically of a conspecific female. According to this hypothesis, the salticid male perceives specifically a conspecific female and it is specifically the perception of a conspecific female that elicits escalation. These two hypotheses are something like the two ends of a continuum of possibilities. That something in between may actually apply is acknowledged, and the following study is best envisaged as a first step toward determining precisely what cues elicit escalation during male-male conflict of *E. parvula.*

MATERIALS AND METHODS

General

All spiders tested were adults from laboratory cultures established by collecting from Donegals Creek, near Kumara Junction (West Coast of the South Island, New Zealand), this being the same site from which the spiders used by Wells (1988) came. Standard rearing and maintenance procedures were used in laboratory under controlled light, humidity, and temperature (lights came on at 0800h and went off at 2000h). For more details, see Jackson & Hallas (1986).

E. parvula is common in the North Island but is also found in the South Island as far south as Christchurch (Forster & Forster 1999). Females are almost uniformly brown, but males have black legs and a red patch on the top of the cephalothorax. Based on the level of risk that appeared likely for a spider performing the display, Wells (1988) ranked the male-male displays of *E. parvula.* Displays that appeared likely to put the displaying male in little or no danger were assigned lower ranks and displays that appeared to expose the displaying male to higher risk of injury (possibly death) were ranked higher. The display adopted by a male was then interpreted as the level of risk this male was willing to incur in a given interaction.

In general, before reaching each successive level, the spiders behaved as described for each earlier level. The level recorded was the highest in the list of six that the losing spider displayed prior to its retreating (without returning).

Wells (1988) recognised five levels of interaction intensity, ranked below from lowest (rank 1) to highest (rank 5).

1. Postured with legs hunched (rank 1). The first three pairs of legs were brought forward, flexed and held close to the body. Adoption of this posture, which will be called the 'hunch display', was usually performed while the two males are distant from each other. This was typically the display first adopted when a male encountered another conspecific male. However, hunch display is not exclusive to early after encounter, but instead, tended to be the dominant display throughout the interaction whenever spiders were at least 10 mm apart.
2. Postured with legs erect while no more than 10 mm from the other male (rank 2). The third pair of legs were held out stiffly above the substrate at about 30° to the horizontal. Often, this display was also used briefly at a distance greater than 10 mm in conjunction with the hunch posture, but at this greater distance it did not qualify as rank 2. While the two spiders were 10 mm or less from each other, this posture (called 'erect display') tended to be maintained for prolonged

periods, during which time the two spiders usually manoeuvred around each other actively.

3. Stave (rank 2). When this occurred the spiders were 5-10 mm apart with legs III erect. To stave, a spider suddenly raised and lowered the erect leg closest to the other male. At the same time the staving spider moved rapidly to one side of the other male, raising the closer side of the body simultaneously while stepping so that when this leg next moved suddenly down it came down against the erect leg of the other male. Staving was often interspersed within bouts during which males manoeuvred around each other, successive lowering of the erect legs coming at intervals of 1-20 s.
4. Embrace (rank 3). The spiders brought the front of their cephalothoraces together and pushed against each other. Legs III often remain erected. Sometimes each spider's erect leg III contacted the other spider's erect leg III. Occasionally, legs I were also erect and touching.
5. Cheliceral-lock display (rank 4). Each spider interlocked its chelicerae with the other male's chelicerae and each spider appeared to attempt to lift the other up. The bodies of the two spiders usually ended up in a tent-like configuration. Occasionally one spider lifted the other off the ground.
6. Fight (rank 5). While the spiders performed the cheliceral-lock display, one male occasionally succeeded in pushing the other male over onto its dorsal surface. Usually the up-ended spider righted itself and ran away. A fight occurred if the rival walked over the up-ended spider, at which point the pair would grapple wildly, venter-to-venter, for several seconds until one male ran away. Fights normally resulted in leg injuries to one or both males, evidenced by immobility of a leg when trying to move after the fight.

Male *E. parvula* courtship displays initially started by posturing with legs hunched interspersed by posturing with the third pair of legs elevated. The legs were normally more tightly hunched during courtship displays than during male-male conflict (i.e., the legs were held closer together so that legs I and II often touched). Courting males also postured by holding legs I erect.

Two types of displays based on movement of the abdomen were adopted during courtship: 'abdomen flip' and 'abdomen dip" (collectively called 'abdomen displays').

'Abdomen flip' started with the abdomen flexed up so that its dorsal surface faced forward and to one side of the cephalothorax. The abdomen was flipped by rapidly moving it from one side of the cephalothorax to the other while simultaneously rotating it so that the abdomen remained facing forward. This normally took between 0.25 and 0.5 s to complete (i.e., to traverse from one side of the cephalothorax to the other). Several abdomen flips sometimes occurred by moving the abdomen from one side of the cephalothorax to the other and back several times. In other instances only one flip was performed at a time.

Prior to an 'abdomen dip' display the abdomen was flexed up and the cephalothorax was lowered. To complete this display the spider flexed the abdomen suddenly down while simultaneously raising the cephalothorax. After pausing for several seconds, the abdomen was then flexed back up.

Two other displays sometimes occurred during courtship, 'sway' and 'wobble'. Swaying was performed by leaning slowly (1-2 times/s) from side to side while posturing with the third pair of legs elevated. The spider's sagittal plane remained perpendicular to the direction of movement throughout this display. Wobbling resembled swaying except the spider also tilted its body around from the rear in the direction the movement, thereby moving the sagittal plane of the body away from the direction of movement.

During courtship, display with legs in the hunched posture was especially common, with elevated-legs display being interspersed. All or some of the above displays occurred during courtship. For more details on courtship displays and the courtship process see Jackson and Willey (1995).

Basic experimental procedure

Encounters between two males were staged in a test arena. This was a Perspex box (215 mm long X 110 mm wide X 30 mm high) with a removable glass top and removable Perspex end pieces. This box was of modular design (see Jackson and Pollard 1990) and could be adapted for use in different types of experiments. For the present study, the arena was shortened to 145 mm long X 110 mm wide X 30 mm high (see Fig. 1 for details of arena set-up) by placing a piece of opaque cardboard (110 mm X 30mm) across the inside of the arena. The arena was shortened to make the dimensions of the arena similar to the arena that Wells (1988) used (i.e., 140 mm long X 110 mm wide X 65 mm high).

Using a fine camel hair paintbrush, one spider was coaxed into the left and the other into the right hand side of the arena (which side for which spider was chosen randomly). The removable Perspex entrance piece (E) was replaced after the spider had entered the arena, thereby preventing the spiders from wandering out of the arena. Great care was taken when moving these animals from their cages, and transferring them into the test arena (and vice versa), to minimise disturbance. Once both spiders were in their separate halves of the arena, interactions were staged by allowing the males (hereafter called the "test spiders") to encounter each other in the test arena. Natural variation in size and coloration made identifying the two individuals in any interaction readily achievable.

All experiments followed a paired-comparison design: the two spiders were tested in the presence of a resource on one day; on the succeeding or preceding day (decided at random), the same pair was tested in the absence of this resource. All tests were conducted between 0900h and 1500h.

The spiders were tested only once within a single 24-h period. No spiders were tested more than twice. When an individual spider was tested twice, it was always paired with a different opponent on the two occasions.

Details about interactions were recorded verbally on audiotape and later transcribed. Details included the number of times the spiders embraced, the distance between the spiders when they first displayed and how close the spiders came to each other during a test. When recording the number of embraces, each individual embrace was defined as ending once the spiders had moved out of contact in the embracing posture for 1 s or more. Also recorded was the maximum rank reached by the loser (i.e. the spider that decamped first and did not return) of an interaction.

Appropriate statistics for pair-wise data were used (e.g., McNemar tests for significance of changes & Wilcoxon tests for paired comparisons: Sokal & Rohlf 1995). The P-values given are after Bonferroni adjustments whenever the same data set are used for multiple comparisons (see Rice 1993).

Experiment 1: Does a moving cork alone influence male-male conflict to escalate?

Wells (1988) investigated male-male conflict in the presence of a moving lure made from a dead conspecific female on a cork. For controls, he staged male-male conflict in the presence of a cork alone, but with the cork stationary. Here I compare the influence of a moving cork with the influence of a stationary cork on male-male conflict. There was no lure of any kind on the moving or the stationary cork (movement was the only variable). The object is to ascertain whether perception of movement, even when what is moving is not a conspecific female, influences male-male conflict.

Methods

Testing began with one male on each side of the arena (Fig. 1). During the experimental test, the cork was moved by

raising the cork approximately 1 mm above the floor and twisting it 90° to the left and then 90° to the right. It took approximately 3 s to twist the cork from starting position to the left then the right and back to the starting position. The spiders tended to orient towards the cork (i.e., move so that its anterio-median eyes were facing towards the cork) quickly. During control tests the cork was raised 1 mm but then left completely still and the divider was not removed until both spiders had their anterio-median eyes oriented towards the cork. This could take more than an hour. However, often both spiders faced the cork surprisingly quickly, possibly because the spiders were coaxed towards the cork when they were introduced the arena.

Once both spiders had oriented towards the cork, the divider was removed and the cork dropped back into the resting position. Recording started when both spiders first displayed simultaneously to one another. If both spiders had not exchanged displays within 30 min after the divider was removed, the test was aborted. The test ended when one spider retreated and did not interact with the other spider within the following minute.

Results and discussion

When the divider was removed, the spiders reacted by turning toward the divider as it was removed. Typically there was a period where the two spiders wandered around the cage. Interactions normally started when one of the spiders oriented toward the other and started to display, with hunched legs, and approached. While approaching, the spider occasionally paused and displayed with erect legs. The second spider would normally turn and face the first spider while the first spider was more than 30 mm away. The second spider usually initiated displays a few seconds after turning and orienting its anterio-median eyes towards the spider that was already displaying.

There was no significant difference between treatments (still-cork and moving cork) in the number of embraces (Fig. 2) (Wilcoxon signed rank test, 2 tailed, P=0.07, N=20), how far apart the two spiders were when the first displayed (Fig. 3) (Wilcoxon signed rank test, 2 tailed, P=0.14, N=20) or how close the spiders came to each other (Fig. 4) (Wilcoxon signed rank test, 2 tailed, P=0.26, N=20). However, spiders in the moving-cork treatment had a significant tendency to reach higher levels than in still-cork treatments (Fig. 5) (Wilcoxon signed rank test, 2-tailed, P=0.03, N=20). What appears to have happened is that interactions were ranked at level 1 when corks were stationary but escalated to level 2 or higher when a cork was moving.

Wells (1988) showed that male-male conflict escalated in the presence of a moving lure (made from a conspecific female). The present experiment shows that the moving object in the environment does not have to be specifically a conspecific female. Even a moving cork without a lure causes interactions to escalate. How to interpret these findings is not clear.

Perhaps stimulation from a moving cork approximately the size of a conspecific female serves, for *E. parvula*, as a cue for the presence of a conspecific female. That is, escalation may indeed function specifically in the context of male-male intrasexual selection, findings from testing with only corks perhaps implying that the cue for presence of a conspecific female is not very exact. An alternative hypothesis is that stimulation from a moving cork-sized object is a cue for something less specific (general-agitation hypothesis).

One interpretation of my findings (and Wells') by the general-agitation hypothesis is that heightened alertness may be adaptive for males in the presence of more or less general-purpose cues that reveal the potential presence of something of significance even when the male does not have information concerning precisely to what the cue pertains. From the male's perspective, it might be a conspecific mate, a conspecific rival, a prey item, a predator, and so forth, but which is indeterminate when the cue is detected.

There are a variety of other potential interpretations of the general-agitation hypothesis, and resolving which applies will require additional research. For example, general agitation might heighten attention to stimuli in

general, including those the males get from each other: escalation, by this interpretation, might come about because the males, once their alertness is heightened by a general purpose cue, notice each other sooner. This interpretation does not link escalation to a conditional strategy of conflict over a resource.

However, there are other interpretations that acknowledge conflict over resources while not requiring that the resource that matters is a conspecific female. For example, escalation upon detecting a general-purpose cue may be adaptive for the male as a general-purpose response (from the male's perspective, some resource or another may be present, but whether it is, for example, a prey or a mate, is uncertain: escalation for either is adaptive). This interpretation can be envisaged as consistent with Wells' (1988), only somewhat weaker than the interpretation he used. However, we cannot rule out a more damaging interpretation: the resource is prey, and any prey-size moving object is, for males, a cue for presence of prey (i.e., males do not resolve the identity of the moving object further than this).

What we know from this experiment and Wells' (1988) study is that in the presence of a moving object *E. parvula* males respond more strongly to each other (by threat displays). We cannot yet rule out that they would also now respond more strongly to predators (by fleeing) or prey (by stalking) in the presence of a moving object. Nor can we draw conclusions yet about how different kinds of moving objects might influence male-male conflict.

Experiment 2: Do optical cues specifically from conspecific females cause male-male conflict to escalate?

The rationale for the next experiment is a hypothesis that more than the general agitation effect is responsible for escalation by *E. parvula* males. If intrasexual selection, with conspecific females being the resource at stake, has driven the evolution of male-male aggression, then males might be expected to escalate the level to which they will go during male-male encounters when they have more reliable information about the presence of a conspecific female. The remarkable acuity of salticid eyes suggest that *E. parvula* would be able to ascertain by optical cues alone that a moving object is specifically a conspecific female.

Methods

The test arena was modified by cutting a notch in the opaque cardboard divider that was used to separate the two test spiders. Otherwise, it remained identical to Fig 1. The notch (approximately 5 mm) was high enough for a lure made from a conspecific female to extend into the arena when the divider was in place, but low enough to obscure the two spiders' view of each other.

A spider was coaxed into one side of the arena (which side was decided randomly) using a fine camel hair paintbrush, and another was placed in the other side of the arena. Which side of the test arena a spider would be introduced was decided at random for each test. Once both spiders were in the arena, either the bare cork (control) or the cork plus the lure made from a conspecific female was moved as in Experiment 1.

Using the methods from earlier studies for making lures (Wells, 1988; Tarsitano & Jackson, 1992; Jackson & Tarsitano 1993; Tarsitano & Jackson, 1994; Tarsitano & Jackson, 1997) was found to be problematic, as the lures quickly deteriorated within the warm humid conditions of the laboratory. I improved on the lures by first freeze-drying the spider to be used as a lure. Using this method, exceptionally life-like long-lasting lures were made.

An adult *E. parvula* female was killed by asphyxiation with CO_2, soaked in ethanol for 1 h, then positioned in a life-like posture on a closed-cell, polyethylene foam (Plastizote) board and held in place with stainless steel pins. Next it was placed overnight into a freezer at –80°C, and then kept in a freeze-drying unit filled with liquid nitrogen for one week under vacuum. After removal from the freeze drier, the lure was glued onto a cork and coated in a transparent varnish spray (Crystal Clear Lacquer, Atsco Australia Pty.) for further preservation and to mask

chemical traces that might have remained on the dead arthropod. The cork on which the lure was mounted was the same size as the cork used in the control (i.e., 25 mm in diameter at its widest point, 20 mm at its finest point, and 40 mm high).

Before the test spiders were placed in the arena, the lure was arranged so that it faced towards the entrance of the arena (E in Fig. 1). In this orientation the lure had its anterio-median eyes towards the viewer and half of its body was on either half of the divider.

Although salticids will react to motionless lures (Jackson and Tarsitano, 1993), they attend to moving lures more readily (Tarsitano and Jackson, 1992). For this reason, there was a preliminary period before the start of each test when the lure was moved until the test spiders were in a position where they both had their anterio-median eyes facing towards the lure. This usually happened within a few minutes. The lure was moved by twisting the base of the cork, so that the lure faced 90° to the left and then 90° to the right. This action was repeated until the divider was removed.

When the spiders were in the desired position the lure was twisted back into the starting position, and the divider was removed. Once divider was removed, the lure was not moved again. The bare cork used during the control test was treated in the same way.

Once the divider was removed, the two males could see each other and interact. Recording started when the two males first displayed to one another. When the divider was removed the spiders usually turned to face the source of the movement (i.e., the divider).

RESULTS

Sometimes, one of the spiders would apparently perceive the lure as a conspecific female, and would be courting the lure before the other spider had oriented towards it. However, it was more common for both spiders simply to be oriented with their anterio-median eyes towards the lure immediately prior to the removal of the divider. Usually one male would spot the other spider moving around the arena, either courting (when a lure was present) or simply walking around on the walls, ceiling or floor of the arena. The first spider seemed to orient towards the movement of the second spider and turned to face the second spider with its anterio-median eyes. Often within seconds of facing the second spider, the first spider started to display, usually by posturing with legs hunched. The displaying spider would approach the second spider and usually tried to manoeuvre so that it approached the front of the second spider. The second spider usually oriented towards this movement, turned to face the displaying spider, and typically adopted a hunched posture a few seconds after facing the displaying spider. Sometimes, the second spider seemed not to see the first spider until the first spider was very close (1-3 mm). This was especially so in two instances where the second spider appeared to be trying to mount the lure. The contests would then progress in a manner similar to that described by Wells (1988) (i.e., progressing in a stepwise fashion through the male-male displays described above from the lowest ranked display to higher ranked ones). Where an interaction was interrupted, as could happen if a displaying spider fell from a wall or the ceiling of the arena, the interaction quickly progressed through lower level displays to the level that occurred before the interaction was interrupted. The interaction would proceed to a certain level of escalation, and then one spider would retreat. If the spiders were still distant, retreating was often by slowly turning and walking away. However, if the spiders were close (i.e., within a few body lengths of each other), then the retreating spider typically retreated by rapidly running away.

The level of escalation reached in an interaction was not significantly different depending on whether a lure made from a conspecific female was present or absent (Fig. 6) (Wilcoxons signed rank test, 2 tailed, $P=0.12$, $N=19$). There was also no significant difference detected in the number of embraces (Fig. 7) (Wilcoxons signed rank test, 2

tailed, P=0.08, N=19). The distance to which a pair of spiders closed did not differ significantly (Fig. 8) (Wilcoxons signed rank test, 2 tailed, P=0.26, N=19). However, *E.* parvula males were found to initiate displays from significantly further away when a female was present than when a female was absent (Fig. 9) (Wilcoxons signed rank test, 2 tailed, P=0.02, N=19).

Experiment 3: Do optical cues specifically from conspecific females cause male-male conflict to escalate when males are courting prior to conflict?

This set of tests is more similar to Wells' (1988) study, than experiment 2, as the males were also required to be courting the lure before removal of the divider. The advantage of the methods used in this set of experiments is that we can be more confident about comparing these results with Wells' (1988) original work. The two major differences between this and Wells' (1988) tests are the slightly smaller test arena in this set of experiments and, more importantly, the addition of movement to the control tests. Experiment 2 cannot be as confidently compared to Wells' (1988) work, as males were not required to court the lure prior to its removal. Experiment 2 does have the advantage that the methods in the control and lure tests are more similar to each other than the control and lure tests in Experiment 3.

Methods

Methods in the second set of lure were similar to those in Experiment 2, the only difference being that in Experiment 3 both spiders had to be actively courting the lure before the divider was removed (see above for a description of behaviours likely to be observed during male courtship displays).

Results

In this experiment the spiders appeared to behave similarly to the previous two experiments, the only noticeable difference being a tendency to continue courting the lure when the divider was removed, rather than turning to towards the movement caused by the divider being removed.

During this set of there was no significant difference in the distance at which the two spiders first displayed (Fig. 10) (Wilcoxons signed rank test, 2 tailed, P=0.15, N=20). Similarly, the number of embraces (Fig. 11) (Wilcoxons signed rank test, 2 tailed, P=0.13, N=20) did not differ significantly between the control tests and tests with a lure made from a conspecific female present. However, the level of escalation an interaction reached was significantly higher in tests when a lure made from a conspecific female was present (Fig. 12) (Wilcoxons signed rank test, 2 tailed, P=0.02, N=20). These results, along with the results from the general-agitation tests (Fig. 5), show a shift from rank 1 displays (i.e., displays performed at a distance) to higher level displays, including displays involving physical contact and fights. Males also approached closer during interactions when a female was present (Fig. 13) (Wilcoxons signed rank test, 2 tailed, P=0.02, N=20).

DISCUSSION

It appears to be appropriate to consider these and Wells' (1988) earlier findings from the perspective of conditional strategies. Conditional strategies are of interest because they potentially reveal specific selection factors that have shaped the evolution of particular behaviour patterns (see Alcock 1998). Studying the rules governing conditional strategies can be envisaged as asking an animal, through experiments, what resources matter to it. In a species with a conditional mating strategy, for instance, each individual has a set of distinct tactics and a set of decision rules specifying the circumstances under which to use each tactic (Dominey 1984). Different tactics appear to be

adaptively fine tuned to the specified conditions. Conditional mating strategies are widespread, if not universal, in the Salticidae (Jackson 1977, 1982b, 1992a). Wells' (1988) study suggests that salticid males also adopt conditional strategies during intrasexual conflict, but the decisions rules in male-male interaction have not been investigated in depth. These decision rules, once clarified, may help explain whether the evolution of male-male conflict in salticids has been driven by intrasexual selection.

Indirectly, by applying game theory, Wells (1988) took these first steps towards clarifying the decision rules adopted by *E. parvula* during male-male conflict. An important prediction from game theory is that the level to which males will escalate conflict is correlated with the value of a resource (Maynard Smith & Parker 1976, Parker & Rubenstein 1981).

Numerous studies on a wide range of animals, including elephant seals (Cox & Le Brouf 1977), spider mites (Potter 1981), red deer (Clutton-Brock 1982), and salticids (Jackson 1980)) have reported higher numbers of injuries and deaths during male-male conflict when a female is present. This is consistent with predictions from game theory and intrasexual selection, making it seem reasonable to suggest that male-male conflict in *E. parvula* may, at least partially, have been shaped by intrasexual selection. This suggestion seems especially reasonable because males of *E. parvula* were found to escalate intrasexual competitions, often with interactions involving physical contact taking place, in the presence of visual cues from a conspecific female, while not usually escalating in the absence of these cues (Experiment 3).

The most extensive work on male-male conflict in spiders is perhaps on male bowl-and-doily spiders, *Frontinella pyramitela* (Araneae: Linyphiidae). Males of this species fight for longer in the presence of conspecific females (Austad 1983). As the danger of male-male combat in this spider species increases with combat duration, Austad concluded that the female bowl-and-doily spider is a resource males are adapted to fight for. Austad (1983) also found that male bowl-and-doily spiders weigh their decisions concerning whether to fight on information based on the reproductive value of a particular female. Reproductive value is defined the number of potentially fertilisable eggs a female carries minus the cost, where cost is a function of the time, risk, and energy necessary to achieve fertilisation of these eggs (Austad 1983). Male bowl-and-doily spiders fought harder for females with higher reproductive value, with virgin females having especially high reproductive value, and less hard for females that had fewer unfertilised eggs.

Another detailed study by Whitehouse (1991) found that males of *Argyrodes antipodiana* (Araneae: Theridiidae), which are kleptoparasitic spiders that build their own webs in the orb webs of other spider species, escalate male-male conflict to higher levels when on conspecific females' webs rather than in the webs of conspecific males.

Wells' (1988) findings therefore might at first appear to be a clear-cut confirmation of a trend that is known in other spiders and for other groups of animals. An interpretation of the findings on *E. parvula* that could strongly imply a conditional mating strategy, where the conditions that matter when two males encounter each other are presence or absence of reliable information on the proximity of a conspecific female. Stated as a hypothesis, males have a rule: when an adult conspecific female is detected, escalate male–male conflict to a higher level (change from 'display at a low level of risk to self' to 'display at a high level of risk to self'). The specificity of the rule would be difficult to explain unless conspecific females really are, as hypothesised, resources that have shaped male-male display behaviour. However, a conclusion that the rule is this specific needs to be supported by additional experimental evidence.

Although not stated explicitly, important assumptions about perception and cognition underlie experimental attempts to test many of the classic game-theory predictions (see Yoerg 1992; Dukas 1998). Wells' (1988) study

was a first step toward testing resource value influencing escalation in a salticid, but interpretation of his findings is problematic because, as often is the case in many studies where game theory predictions are tested, there are numerous potentially important uncontrolled variables.

An assumption in Wells' (1988) study would seem to be that *E. parvula* males can by eyesight alone, perceive when a lure made from a conspecific female is present. The extraordinary visual acuity of salticids (Land 1969a,b; Blest et al. 1990; Jackson & Harland 1998; Harland et al. 1999) suggests that they are the one group of spiders for which this assumption is reasonable, but experimental confirmation is essential. Wells (1988) had a moving lure made from a conspecific female in experimental tests but only a motionless cork was present during his controls, leaving open the possibility that movement of a cork-size object alone was sufficient to cause interaction escalation. The following experimentation aimed to examine this assumption.

Experiment 1 showed that movement of a cork alone, in the absence of a lure made from a conspecific female, causes *E. parvula* males to escalate conflict to a stage involving physical contact (presumably incurring increased risk of injury). From the results of Experiment 1 we can therefore conclude that the escalation in Wells' (1988) study of male-male conflict in *E. parvula* can be attributed to a general-agitation effect caused by movement of the lure Wells used as his control stimulus.

In the first of the lure experiments (Experiment 2), where courting was not required before removal of the divider, no escalation to higher ranked behaviours was detected. However, the presence of a lure made from a conspecific female does have a significant effect on male-male conflict in *E. parvula*. In experiment 2, a lure made from a conspecific female causes males of *E. parvula* to initiate displays from a greater distance compared with tests in the absence of optical cues from the lure. An alternative interpretation of this result, that the absence of a female causes males to approach closer before displaying to each other, is unlikely. It seems unlikely that optical cues from a bare cork would somehow inhibit the onset of intrasexual display by males of *E. parvula* while optical cues from a cork plus a lure made from a conspecific female have no comparable inhibiting effect. A more likely scenario is that seeing the lure somehow primes the males to detect optical cues from each other sooner.

Something similar to this has been shown in another system. When *Portia fimbriata,* from Queensland, Australia, detects chemotactile or olfactory cues from *Jacksonoides queenslandicus,* a salticid on which it frequently preys, it attends to optical cues from *J. queenslandicus* faster (Jackson et al in prep.). Evidence for increase in attention includes increased likelihood of stalking a lure made from *J. queenslandicus*, initiating stalking of the lure sooner, and approaching closer to the lure when these cues from *J. queenslandicus* are present compared with when these cues are absent. Something analogous may be occurring in Experiment 3, but here the priming cues are optical. In other words, *E. parvula* males detect optical cues from a conspecific female that somehow act to prime these males to detect optical cues from other conspecifics faster than normal). From this experiment we cannot tell how specific this is. Possibly cues from any conspecific would prime *E. parvula* of either sex to detect optical cues from another conspecific faster than would normally occur (hypothesis 1). Alternately (hypothesis 2), it may be only cues from *E. parvula* females that prime *E. parvula* males to detect optical cues for other conspecific males more readily. Hypothesis 2 is the most clearly compatible with intrasexual selection, as faster detection of rival conspecific would provide males with information they can use as an aid in the contests over mating opportunities.

Escalation occurred in Experiment 3, where *E. parvula* males were tested in the presence and absence of a lure made from a conspecific female, where a requirement was that the two males were courting before removal of the divider. Escalation occurred in Experiment 3 even though movement occurred in all tests. If general-agitation effects from movement from a cork sized object was the only influence, then the findings from Experiment 3 would not have been expected. The results of Experiment 3 and, to a lesser extent, Experiment 2 suggest that *E. parvula*

males are influenced by more than simple movement of a cork-size object.

Escalation up to the stage that physical interactions occurred in only one of the experiments designed to study the effect of optical cues from a lure made from a conspecific female on intrasexual conflict in male *E. parvula*. When males of *E. parvula* were courting the lure, prior to encountering another male, conflict escalated by increasing to higher ranked (and presumably more dangerous) behaviours, compared to interactions where no lure was present. Also, in these experiments spiders approached closer during interactions when a lure was present than during those interactions where only a bare cork was present.

Results from Experiments 2 and 3 might have differed because some of the spiders did not see (or else saw but did not recognise) the lure in Experiment 2. In Experiment 2, we cannot be completely certain that the *E. parvula* males had seen the lure, and if they saw it, had recognised it for what it was. Salticid-eye fovea have narrow fields of view and the eyes tubes do not always point straight ahead (Land 1969a, b; Blest et al 1990; Harland & Jackson 2000). Therefore, one cannot be sure that a salticid has brought an image onto the fovea simply because something is in front of its anterio-median eyes. Also, for salticids, perception appears to be based on scanning the image using highly mobile eye tubes and this may be a slow process (Harland & Jackson 2000). Therefore, we cannot be sure the lure (or cork) was seen in Experiment 2 because the only requirement was that the males had to have their front end oriented towards the lure (or bare cork).

However, in Experiment 3, where courting was required before male-male interaction was initiated, we can be sure that the spiders had seen the lure and had ascertained that it was a female. By requiring the spiders were courting the lure, we can be sure that the males 'knew' a conspecific female was present because *E. parvula* males perform courtship displays only in the presence of a female (Jackson & Willey 1995). Therefore, even though the act of displaying itself somehow makes the males more aggressive, we can still be confident that the escalation observed in Experiment 3 is at least indirectly due to the presence of the female.

The experiments in the present chapter have taken Wells' (1988) study a step further, but they raise finer-grain questions about additional uncontrolled variables. In Experiment 3, a moving lure made from a conspecific female was present, but only a moving bare cork was present in control tests. Therefore, we cannot say that *E. parvula* males perceived, using optical cues, specifically a conspecific female and made decisions concerning escalation on this basis. It may be tempting to say that, because the males were performing courtship displays toward the lure, they must have perceived the lure as specifically a conspecific female. However, refinements of the general-agitation hypothesis, for example, have not been ruled out. For example, it might be that males perceive the lure as a member of some broader category (e.g., something that might be a mate, a prey or a predator) that causes general agitation of the male. We may be closer than with Wells' (1988) study alone to showing that escalation is a decision made as part of a conditional strategy, with the function being in the context of intrasexual selection, but further study is needed before this can be concluded with a high degree of confidence. One approach might be to make systematic changes in the control stimulus. Instead of this, another research strategy and another set of questions were adopted to refine how we can interpret male-male conflict in the Salticidae (see Chapters 3-5).

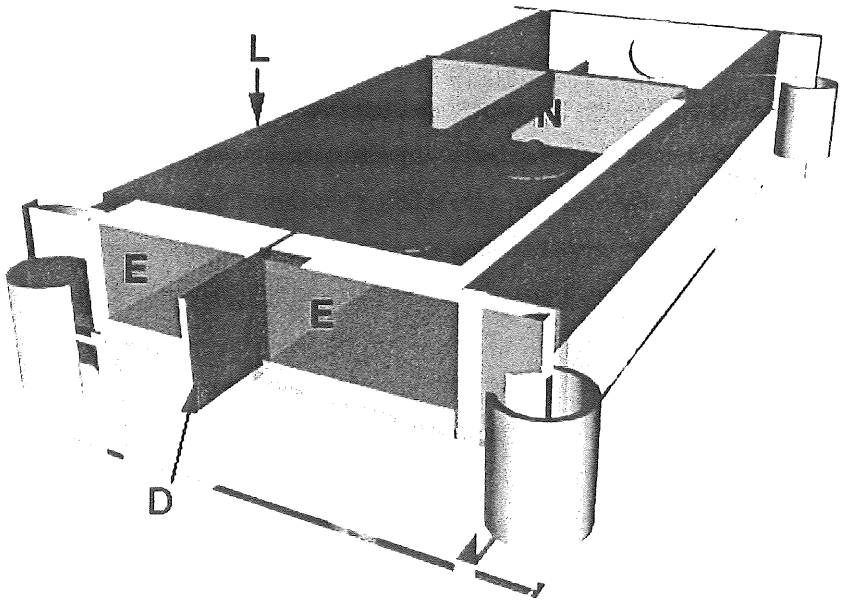

Fig. 1: Drawing of transparent Perspex "modular cage". C: Cork that plugged a hole in the floor of the arena, and provided movement during tests (except during the general agitation control tests). A lure was mounted on a cork, the same size as the one shown, and used during the experimental component of the lure test (lure not shown). D: Opaque cardboard divider bisected the arena, which allowed spiders to be placed one on either side of the area and allowed both animals to see the cork (and lure, if present) without seeing each other. E: Clear Perspex end pieces that were removed to allow the spiders into one half of the arena and replaced to keep spiders in the arena. These end pieces were held in place by plastic clamps. L: Transparent glass lid that formed the roof of the arena that allowed observation but prevented the animals from escaping. N: Notch cut into the divider to allow the lure to be mounted on the cork and be seen on both sides of the arena (not present during the general agitation tests).

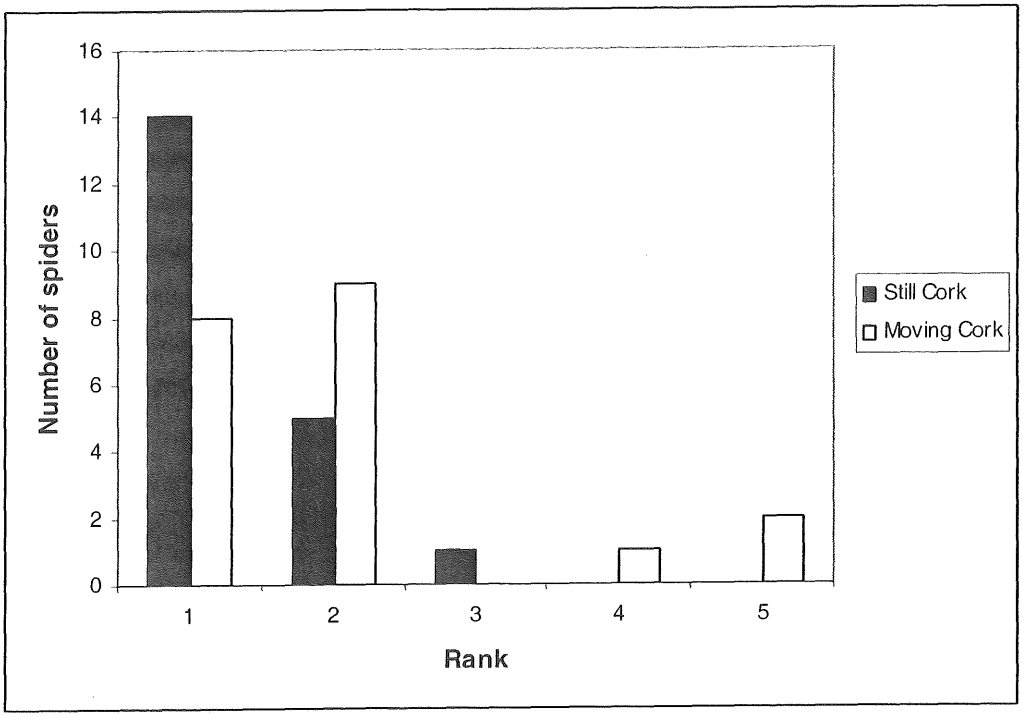

Fig. 2: Number of contests (N=20) at each level of escalation. Tests with a still cork versus tests with a moving cork.

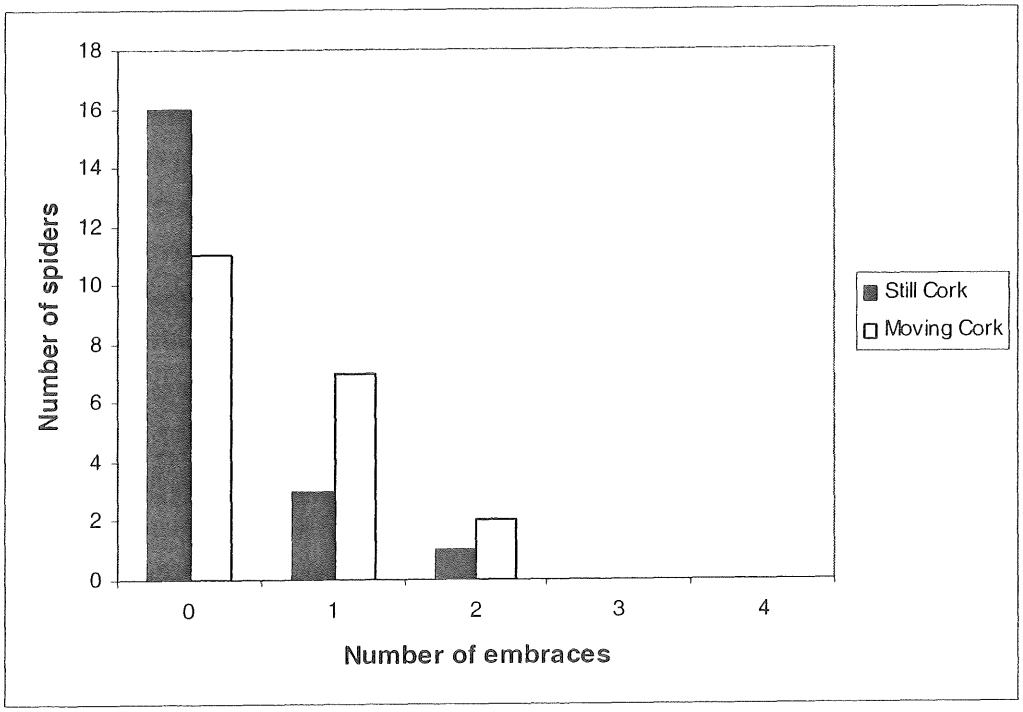

Fig. 3: Number of embraces in each contest (N=20). Tests with a still cork versus test with a moving cork.

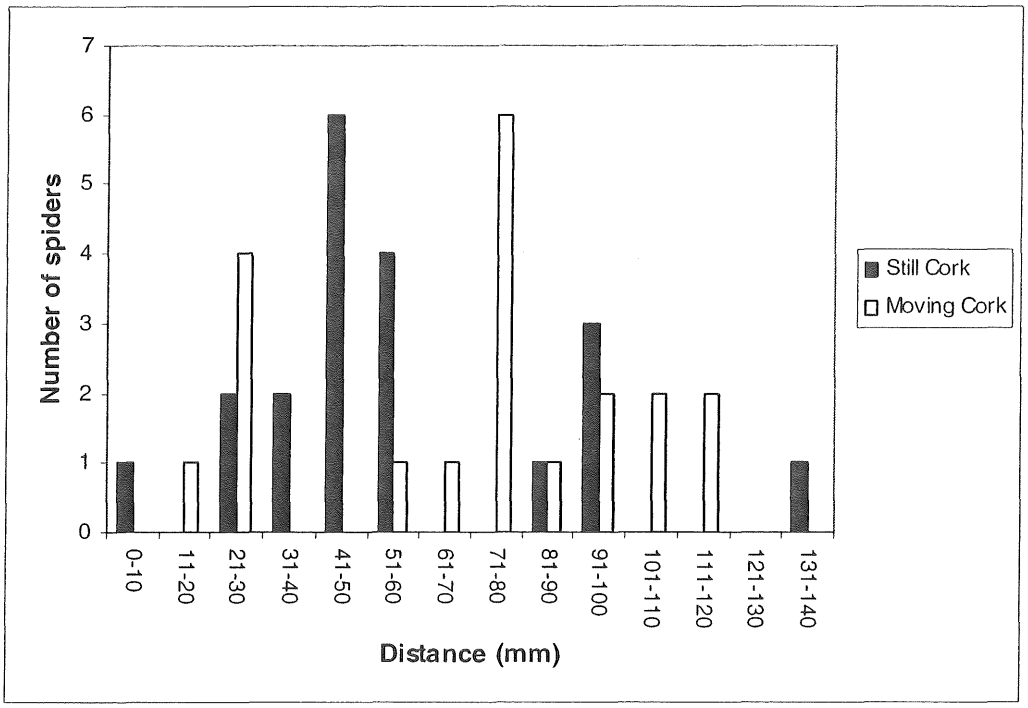

Fig. 4: Distance at which a pair of spiders first displayed comparison of tests with a still cork versus tests with a moving cork (N=20).

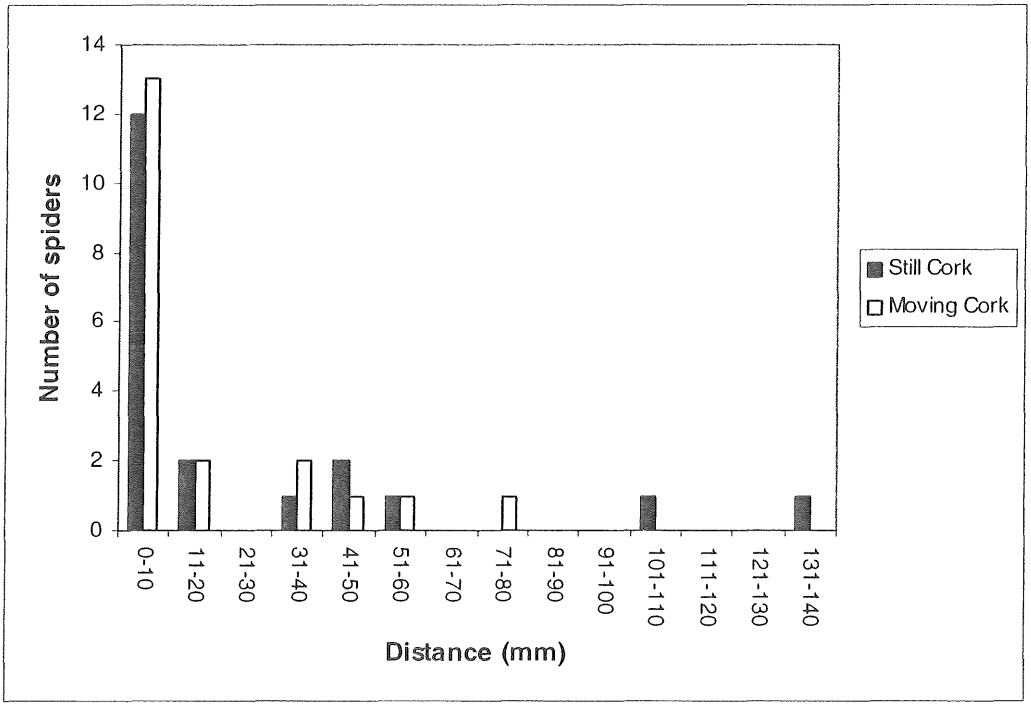

Fig. 5: Comparison of the distance a pair of spiders closed to in tests with a still cork versus tests with a moving cork (N=20).

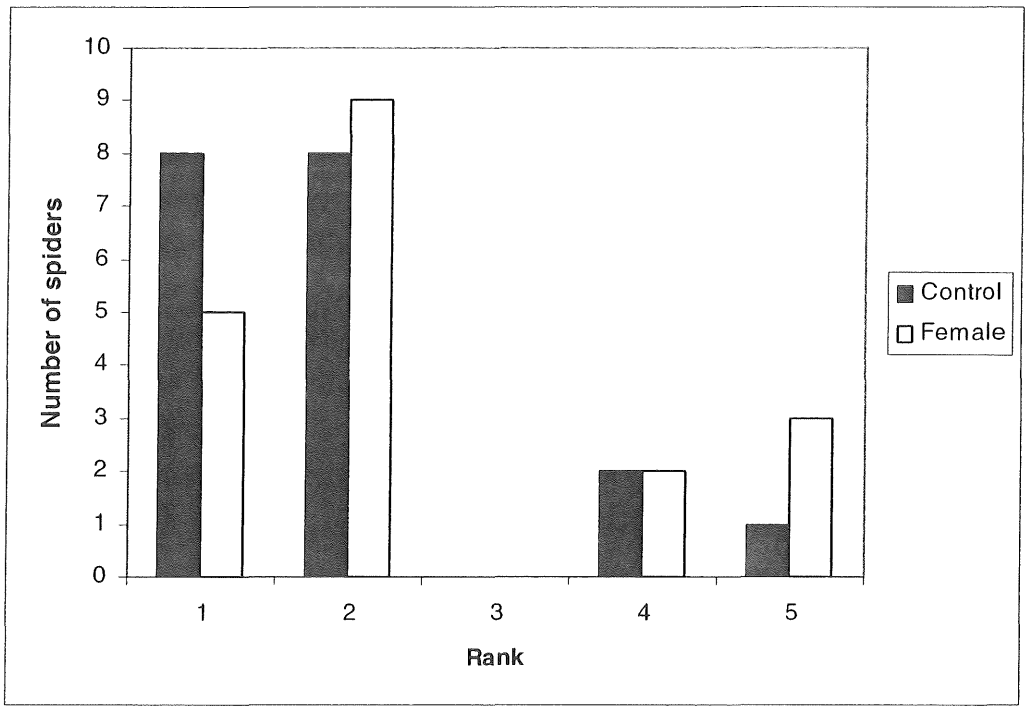

Fig. 6: Number of interactions (N=19) at each level of escalation with lure (made from conspecific female) present and absent. Males did not court lure before male-male interaction occurred.

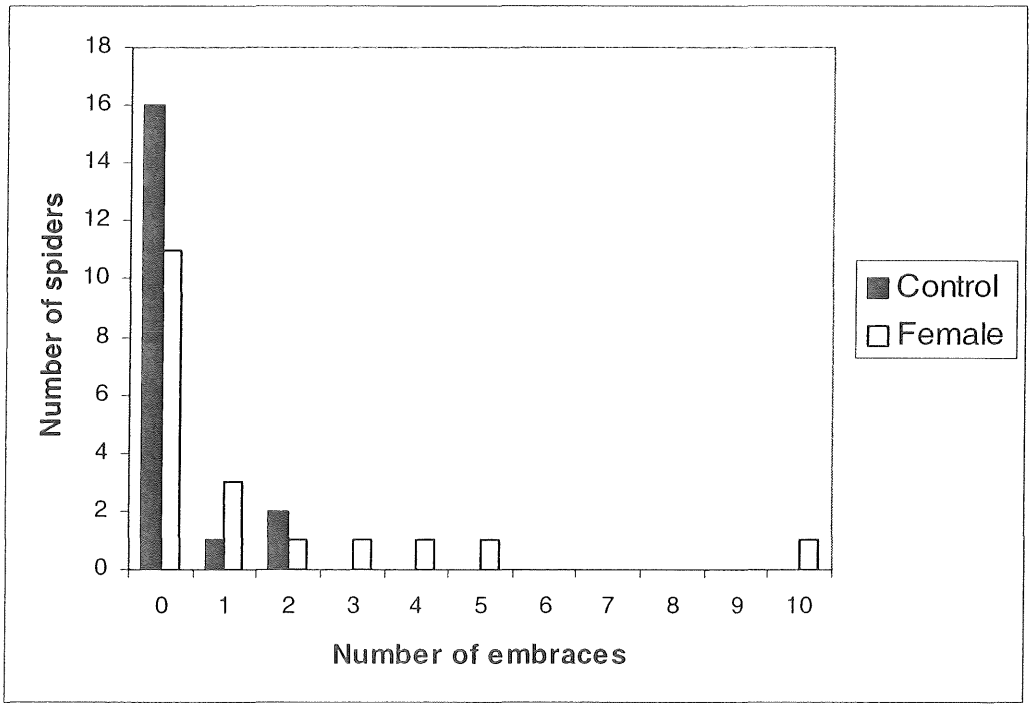

Fig. 7: Number of embraces in each interaction (N=19) with lure (made from conspecific female) present and absent. Males did not court lure before male-male interaction occurred.

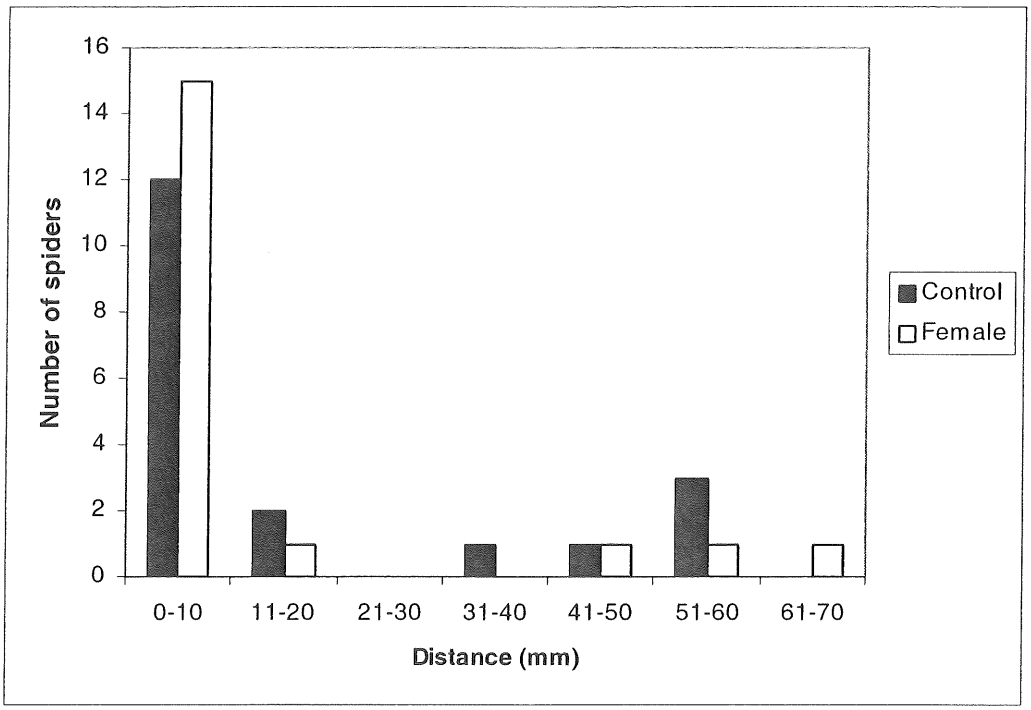

Fig. 8: Comparison of distance a pair of spiders would close to in tests with lure (made from conspecific female) present and absent (N=19). Males did not court lure before male-male interaction occurred.

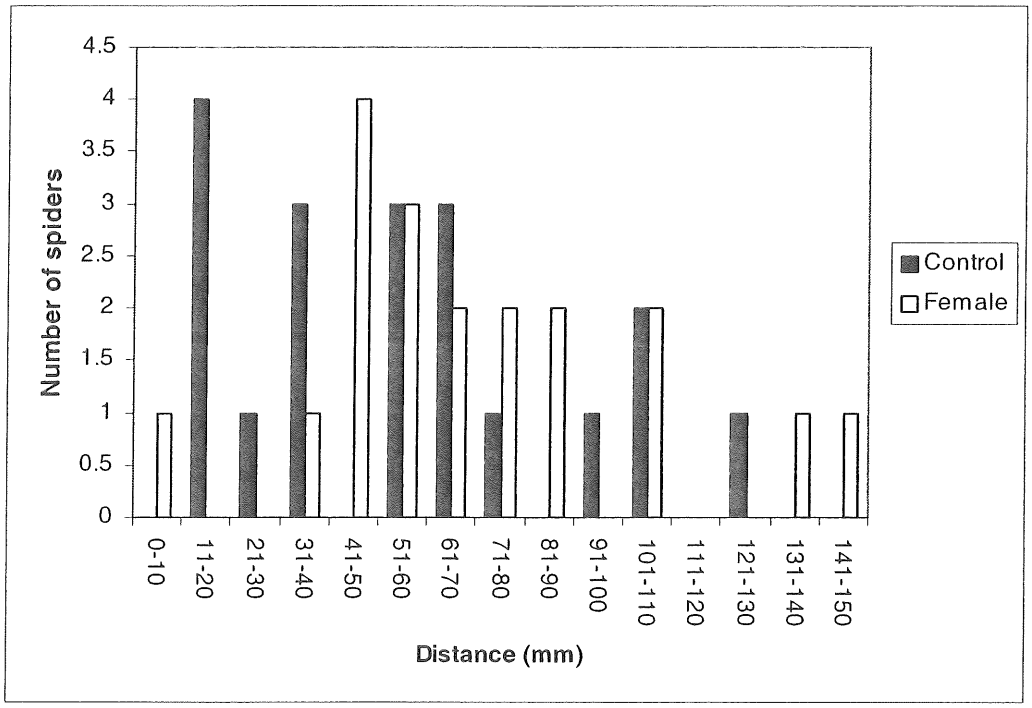

Fig. 9: Comparison of distance at which pairs of spiders first displayed with lure (made from conspecific female) present and absent (N=19). Males did not court lure before male-male interaction occurred.

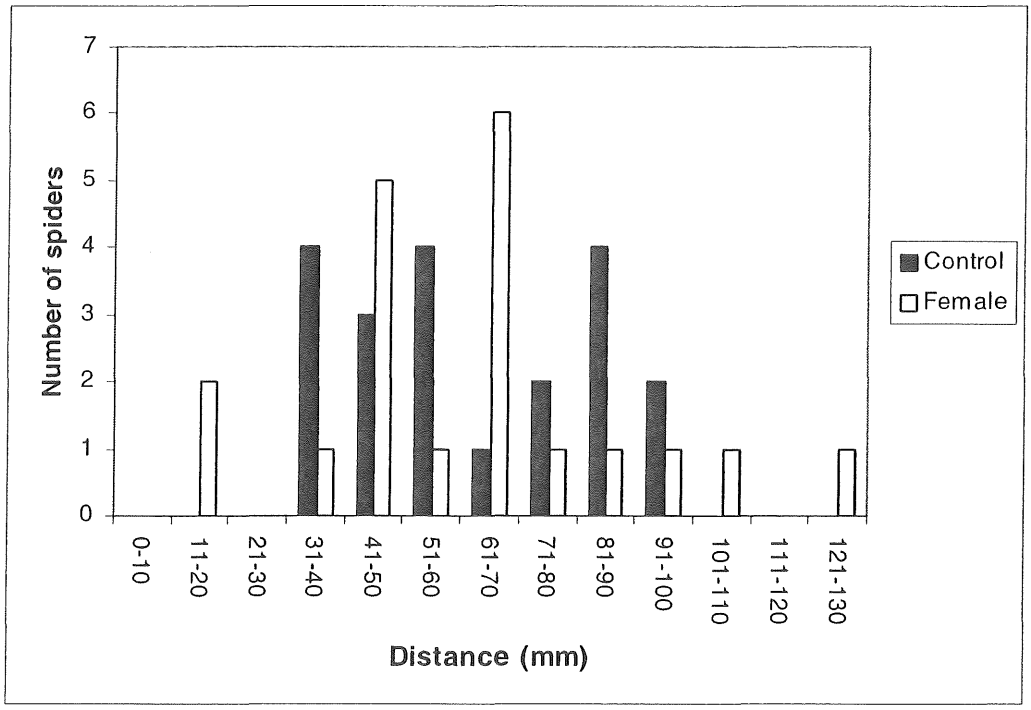

Fig. 10: Comparison of distance at which a pair of spiders first displayed with lure (made from conspecific female) present and absent (N=20). Males courted lure before male-male interaction occurred.

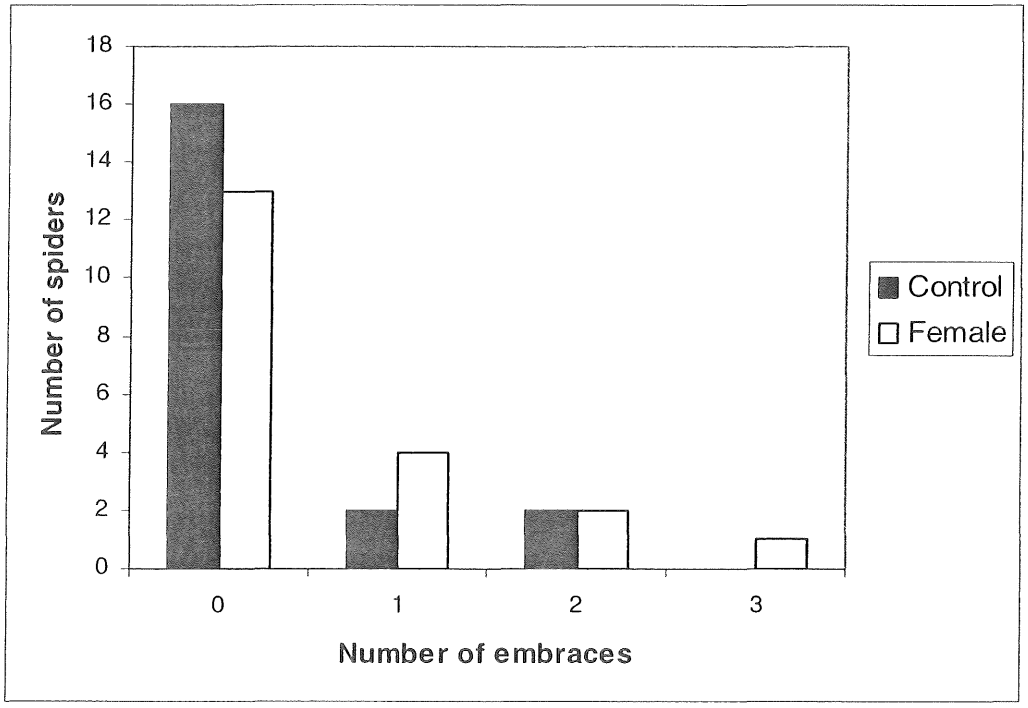

Fig. 11: Number of embraces in each interaction (N=20) with lure (made from conspecific female) present and absent. Males courted lure before male-male interaction occurred.

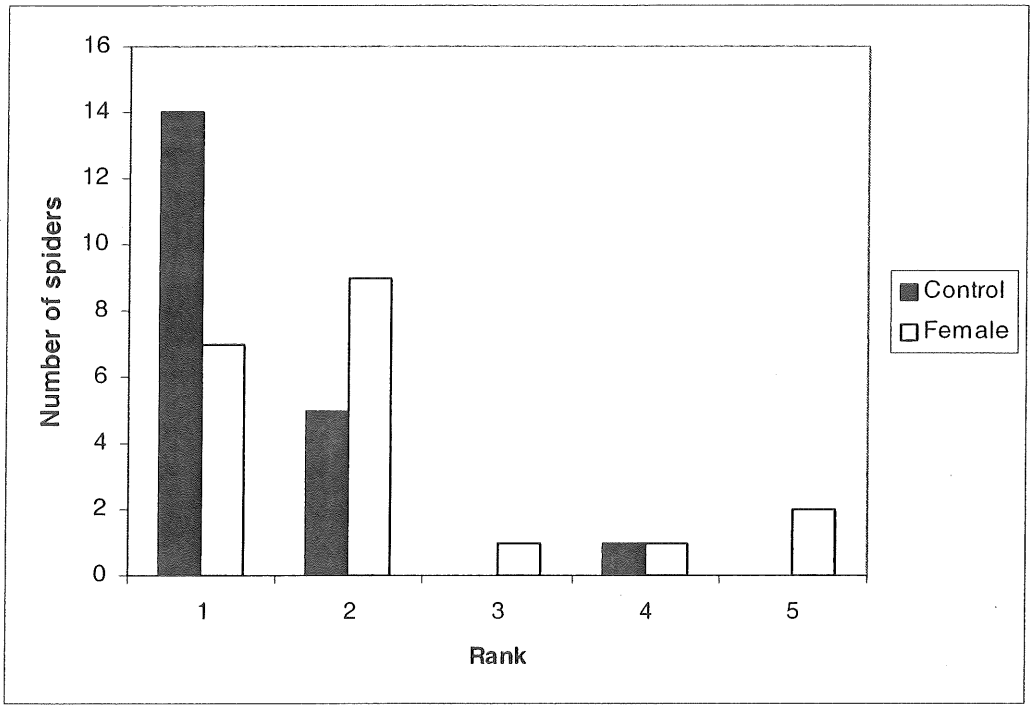

Fig. 12: Number of contests (N=20) at each level of escalation with lure (made from conspecific female) present and absent. Males courted lure before male-male interaction occurred.

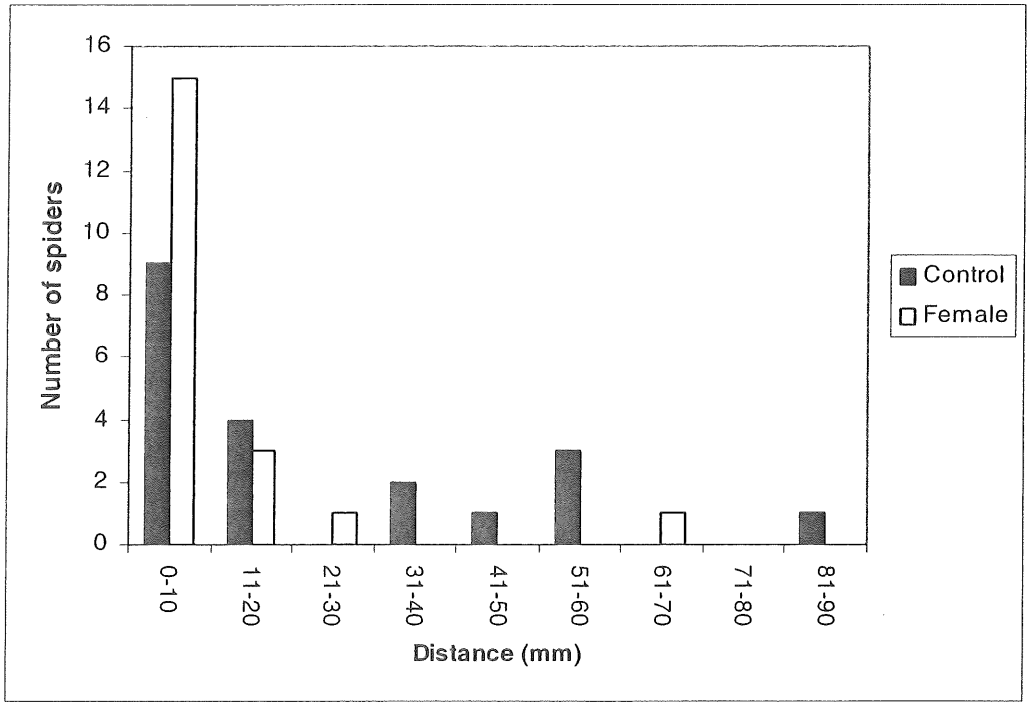

Fig. 13: Comparison of distance to which a pair of spiders closed in tests with lure (made from conspecific female) present and absent. Males courted lure before male-male interaction occurred.

Chapter 3: The influence of optical cues on male-male conflict in *Jacksonoides queenslandicus* and *Portia fimbriata*, jumping spiders from Queensland, Australia.

INTRODUCTION

Most spiders have simple eyes that do not support high-acuity vision, but salticids have unique, complex anterio-median eyes that support resolution abilities, with no known parallels in other animals of comparable size (Land 1969a; Land 1969b; Blest et al. 1990; Jackson & Harland 1998; Harland et al. 1999). Not surprisingly, salticid spiders are cursorial predators that actively hunt their prey using vision-guided predatory sequences (Forster 1982a; Jackson & Pollard 1996; Harland & Jackson 2000).

Vision also plays a major role when salticids communicate with conspecifics (Jackson 1982a). The often intricate postures and displays seen when conspecifics meet can be split into two categories depending on the sex of the two interacting spiders. The function of 'courtship' displays (Richman & Jackson 1992), which occur when an adult male salticid encounters an adult conspecific female, seems to be to persuade the conspecific female to mate with the male (Richman 1982; Jackson & Pollard 1997). Female mate-choice behaviour may have driven the evolutionary elaboration of male courtship displays. Although saying that intersexual selection explains the evolution of courtship displays would be overly simplistic, there is at least limited evidence that females do choose particular males with which to mate on the basis of male display (Jackson 1982b; Jackson & Pollard 1997).

When an adult male salticid meets another conspecific adult male, the displays that occur differ from those used during courtship. Intrasexual display differs from courtship display by appearing more 'aggressive'. For example, the forelegs are hunched and the fangs are often exposed (Jackson & Pollard 1997). Male-male interaction may escalate up to the point of physical contests during which one or both individuals may be injured or even die (Wells 1988; Faber & Baylis 1993). Despite male-male display being a distinctive feature of salticid behaviour, often called 'aggression' for short, we only poorly understand why males engage in this behaviour (Jackson & Cooper 1991; Pollard 1994; Pollard 1995).

It has become common to suggest that this intense male-male conflict is due to intrasexual selection pressure where male salticids are directly competing with one another for access to mates. This hypothesis seems especially appealing because male-male conflict is generally much more pronounced than female-female conflict (longer in duration, more often progressing to contact behaviour and more often resulting in injury or death) (Jackson & Pollard 1997).

However, the role of intrasexual selection (if there is one) in salticid male-male conflict is ambiguous, partly because clear evidence is lacking on whether salticid male-male interactions fit any of the better-known patterns associated with intrasexual selection in other animals, such as social dominance, resource-based territoriality or leks (Gould & Gould 1989; Andersson 1994). With salticids, the relationship between intrasexual conflict and intrasexual selection needs to be identified and defined. Mark Wells (1988) studied male-male conflict in a New Zealand jumping spider, *Euophrys parvula*, and discovered escalation of aggression in male-male conflict when visual cues from a lure made from adult conspecific female was present. This study would appear to be a first step toward showing that intrasexual selection has shaped male-male conflict in salticids. Wells' (1988) study was based on game theory, a prediction of which is that intensity of conflict will increase if a limiting resource is present (Maynard Smith & Parker 1976, Parker & Rubenstein 1981; Maynard Smith 1982). Wells' (1988) study might be interpreted as showing that, during male-male conflict, conspecific females are a resource being competed for (i.e., that male-male conflict is driven by intrasexual selection).

However, in Chapter 2, another factor, a 'general-agitation' effect, was shown to be potentially important. The general-agitation effect (from simply being exposed to a moving object) suggests that more or less any extraneous stimulation might put salticid males in a state of heightened arousal. If a salticid male encounters another conspecific male while in this heightened state of arousal, heightening of aggression during intrasexual conflict may be something like an artefact.

However, when Wells' (1988) experiment was repeated, with the addition of a control for movement, his results were duplicated (Chapter 2). Whether the findings from experiments using *Euophrys parvula* males (Wells 1988; Chapter 2) apply to males of other salticid species is unknown. Here I investigate, using the same methods as in experiment 3 in Chapter 2, another two salticid species, *Portia fimbriata* and *Jacksonoides queenslandicus*, both of which are from rainforest habitats in Queensland, Australia. The biology and display behaviour of these species are known from earlier studies (Jackson & Blest 1982; Jackson 1988).

MATERIALS AND METHODS

General

All spiders tested were adults from laboratory cultures established by collecting from the tropical rainforests in the vicinity of Cairns, North Queensland, Australia. Standard rearing and maintenance procedures were used in a controlled-environment laboratory. Lights came on at 0800h and went off at 2000h. For more details see Jackson & Hallas (1986). All testing occurred between 0900h and 1500h. Because male-male conflict tests were in basic respects the same as described elsewhere (Chapter 2), only essential details will be provided plus information about the display behaviour of the two species of test spider, *P. fimbriata* and *J. queenslandicus*. The rationale for ranking levels of intensity reached in male-male interactions follows Chapter 2 and Wells (1988).

Description of displays and ranking

Only brief descriptions of intrasexual behaviour are given here, but details for both species can be found elsewhere (Jackson 1982c; Jackson & Hallas 1986; Jackson 1988). Rankings are listed from lowest intensity to highest intensity.

1) *Portia fimbriata*.

1. Posturing with legs hunched (rank 1). The first three pairs of legs were brought forward, flexed and held close to the body. Adoption of this posture, which was called the 'hunch display', was usually performed while the two males were distant from each other, and was typically the display first adopted when a male encountered another conspecific male. However, hunch display was not exclusive to early in encounters, but instead tended to be the dominant display throughout the interaction whenever spiders were at least 10 mm apart.
2. Posturing with legs erect (rank 1) while no more than 10 mm from the other male (rank 2). The first pair of legs alone, or more often the first two pairs of legs together, were held out stiffly above the substrate at about 45° to the horizontal and were angled between 45-90° out to the side of the males' body. This display was often used briefly at a distance greater than 10 mm in conjunction with the hunch posture, but at this distance it did not qualify as rank 2. While 10 mm or less, from each other, this posture (called 'erect display') tended to be maintained for prolonged periods, during which time the two spiders usually manoeuvred around each other actively.
3. Embrace (rank 3). The spiders brought the front of their cephalothoraces together and

pushed against each other. As the spiders approached the erect legs of the two spiders displaying overlapped as they got closer. The cephalothoraces of the two spiders were often raised, with the abdomen tilted down. These displays only lasted 5-10 s.

4. Grapple (rank 4). Embracing spiders grappled by moving their overlapping forelegs forward over the opponents' forelegs and forcefully flexing these legs. This display sometimes pulled off one of the opponent's legs.
5. Fight (rank 5). While embracing one male occasionally pushed the other male over onto its dorsal surface. Usually, the up-ended spider righted itself and ran away. However, a fight occurred if the rival spider walked over the up-ended spider. The pair fought by grappling wildly until one male ran away several seconds later. While fighting, the spiders were venter-to-venter.

P. fimbriata males usually initiated courtship displays, directed towards the lure made from a conspecific female, by posturing with legs erect. The erect leg display seen in courtship displays differed from a similar erect legs display that occurred in male-male conflict. The erect leg display that occurred during courtship was characterised by the males extending legs 1 forward in front of the other spider. With these legs approximately parallel to the floor of the arena, the male approached the female while waving legs 1 (raising and lowering each leg in alternate phase: i.e., when the left leg was at the peak of the oscillation the right was at the bottom of the oscillation). The legs moved 1-3 mm vertically during each oscillation, and took approximately 1 s to complete one oscillation.

2) *Jacksonoides queenslandicus.*

1. Posturing with legs hunched (rank 1). The first three pairs of legs were held highly flexed and to the side of the body (perpendicular to the sagittal plane of the body). Adoption of this posture (hunch display), was usually while the two males were distant from each other and was typically the display first adopted when a male encountered another conspecific male. However, hunch display was not exclusive to early after encounter, but instead tended to be the dominant display throughout the interaction at any time when the spiders were at least 10 mm apart.
2. Posturing with legs erect (rank 1) while no more than 10 mm from the other male (rank 2). The first pair of legs alone, or sometimes first two pairs of legs, were held out stiffly above the substrate (10-45° to the horizontal) and were angled approximately 45° directly from forward. (This display was often used briefly at a distance greater than 10 mm in conjunction with the hunch posture, but at this distance did not qualify as rank 2.) While 10 mm or less, from each other, this posture (called 'erect display') tended to be maintained for prolonged periods, during which time the two spiders usually manoeuvred around each other actively.
3. Embrace (rank 3). The spiders brought the front of their cephalothoraces together and pushed against each other. The first pair of legs were held erect out from the side of the body and usually remained in contact with the opponents' legs I during this display. Embraces were often performed briefly (1-2 s in duration) with bouts of short-duration, repeated embracing sometimes occurring.
4. Wrestle (rank 4). Wrestling occurred while the spiders embraced. The two spiders locked their chelicerae (with fangs not exposed) and twisted their cephalothoraces alternately clockwise then anticlockwise (about 20° in each direction).

5. Fight (rank 5). Fights between the two male *J. queenslandicus* followed a similar pattern to that found in fights between male *P. fimbriata*. Fights usually occurred directly after wrestling and involved the two spiders grappling venter-to-venter. Like fights between *P. fimbriata* males, one *J. queenslandicus* male would normally decamp rapidly thus ending the fight.

When *J. queenslandicus* males started courting the lure made from a conspecific female, they routinely began with the erect display. As a male approached the lure, his first pair of legs shifted so that they extended forward and parallel to the floor of the arena. As the male approached closer, the first pair of legs were suddenly and rapidly flicked up and down. Flicks were performed (in bouts of 2-4 s in duration, legs raised and lowered 1-2 mm) rapidly (2-4 flicks/s) in alternate phase.

Basic experimental procedure

Encounters between two adult conspecific males were staged the test arena (144 mm long X 110 mm wide X 30 mm high) used in experiments 2 and 3 of Chapter 2 (Fig. 1). These male-male encounters were of a paired-test design with each spider tested in the presence and in the absence of optical cues from a lure made from an adult conspecific female.

Lures were made from adult females of *P. fimbriata* and adult female *J. queenslandicus* that had been asphyxiated with CO_2, soaked in ethanol, dried and mounted in a lifelike posture and then freeze-dried. Following freeze-drying, the lure was glued to a cork (25 mm at the widest point, 20 mm at the finest point and 40 mm high) and coated with an aerosol plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty).

The spiders were only tested once within a single 24-h period. No spiders were tested more than twice. When an individual spider was tested more than once, it was always paired with a different opponent.

The males were put on either side of the opaque cardboard divider that split the test arena into two. This divider was placed so that the lure was visible to the two test spiders, but still obscured the spiders from each other. During the experimental tests the lure was moved until both test spiders were courting the lure. When both spiders were courting the lure, the divider was removed. Removing the divider allowed the test spiders to interact.

The control test was conducted in a similar way, except that only a bare cork (25 mm at the widest point, 20 mm at the finest point and 40 mm high) was present instead of a lure. The cork was moved until both spiders had turned so that their anterio-median eyes were oriented toward the cork. The spiders were not required to court the bare cork. Once both spiders were facing the cork the divider was removed.

Although, the general-agitation effect was not tested for these species (i.e., the equivalent of Experiment 1 in Chapter 2 was not carried out), the possibility of this effect was controlled by having movement occur in both the control (bare cork) and the experimental (cork plus lure) tests.

A test started when the two spiders first exchanged displays. If both spiders had not displayed within 30 min after the divider was removed, the test was aborted. The test ended when one spider retreated and did not return or the spiders lost interest in each other (definition: both spiders stopped displaying and either wandered away or became quiescent).

The details about interactions (the number of times the spiders embraced, the distance between the spiders when they first displayed and how close the spiders came to each other during a test) were recorded verbally on audiotape and later transcribed. Also recorded was the maximum rank of the loser (i.e. the spider that decamped first and did not return) of a contest. This determines the level of escalation of a given conflict and enable comparison between the control and experimental tests.

Appropriate statistics for pair-wise data were used (e.g., McNemar tests for significance of changes & Wilcoxon tests for paired comparisons: Sokal & Rohlf 1995). The P-values given are after Bonferroni adjustments whenever the same data are used for multiple comparisons (Rice 1993).

RESULTS

When the divider was removed, the spiders did not usually react to this movement, but instead continued to court the lure. Alternately, they sometimes paused, turned briefly towards the divider, and then resumed courting the lure. Generally, one male would be closer to the lure than the other. Interactions normally started when the male furthest from the lure stopped performing courtship displays and turned to orient towards the courting male. After a short pause, the first spider typically adopted a hunched posture and advanced towards the second spider. As the first spider approached, it appeared to be attempting to manoeuvre around to the front of the second spider. The second spider typically stopped courting the model and turned towards the first spider before it had moved in front of the second spider. The second spider usually postured with hunched legs soon after orienting its anterio-median eyes. Once both spiders were displaying to one another, they continued to display until one spider retreated, thereby ending the interaction. In no test did spiders interrupt male-male interactions to court the lure.

In most instances the male-male interactions of *P. fimbriata* were limited to visual displays (i.e., rank 1 or 2). However, there were more instances of physical displays in tests with a lure made from a conspecific female present compared with tests in the absence of the lure (Fig. 14). The level of escalation in *P. fimbriata* male-male conflict in the presence of a lure was significantly different when compared with the level of escalation observed in absence of the lure (Wilcoxon's signed ranks test, 1 tailed, P=0.05, N=20).

However, no other variables recorded during interactions provided evidence of a significant effect on male-male conflict in the presence of a lure made from a conspecific female compared with the absence of the lure. The pairs of spiders did not differ significantly in the number of embraces that occurred between the experimental and control tests (Fig. 15) (Wilcoxon's signed ranks test, 1 tailed, P=0.13, N=20). Also, there was no significant difference in the distance at which the spiders first displayed to one another (Fig. 16) (Wilcoxon's signed ranks test, 1 tailed, P=0.09, N=20). Similarly, the distance the spiders closed to during control and experimental treatments did not differ significantly (Fig. 17) (Wilcoxon's signed ranks test, 1 tailed, P=0.33, N=20).

Like male *P. fimbriata*, male *J. queenslandicus* reacted to the removal of the divider by either continuing courtship or by turning towards the movement of the divider being removed. It appeared to be the case that a greater proportion of *J. queenslandicus* males, compared with *P. fimbriata* males, turned towards the divider as it was removed, but data on this was not tested. As with *E. parvula* (Chapter 2) and *P. fimbriata* males, intrasexual interactions between male *J. queenslandicus* normally began when one male turned towards the second male while the second male was courting the lure. The first male started to display by posturing with hunched legs, and attempted to move around to in front of the second male. The second male often turned towards the displaying male before it had manoeuvred in front; the second male usually started to display within a few seconds of turning toward the first male.

For *J. queenslandicus*, most male-male conflict in this set of experiments did not escalate beyond the visual displays (i.e., rank 1 displays) (Fig. 18). Only two tests escalated to physical contact and both of these interactions a lure made from a conspecific female was present. However, the control and the experimental tests were not significantly different (Wilcoxon's signed ranks test, 1 tailed, N=20) because there were too many untied tests to calculate the Wilcoxon statistic. Similarly, the number of embraces (Fig. 19) did not differ significantly (Wilcoxon's signed ranks test, P=0.25, N=20) between the control and experimental contests. This was probably a consequence

of how rarely escalation to physical interactions occurred (the median number of embraces in both the control and lure test was 0). There was no significant difference in the distance that the spiders first displayed to each other (Fig. 20) (Wilcoxon's signed ranks test, 1 tailed, P=0.45, N=20). The distance the spiders closed to during an interaction (Fig. 21) (Wilcoxon's signed ranks test, 1 tailed, P=0.14, N=20) was also not significantly different between the tests where a lure made from a conspecific female was present compared with tests where the lure was absent.

DISCUSSION

This chapter, Chapter 2 and Wells' (1988) earlier work are the first steps toward understanding the decision rules that govern intrasexual conflict in salticids. Game theory predictions have been used to help clarify these decision rules. An important prediction from game theory is that the level to which males will escalate competitions is positively correlated with the value of a resource (Maynard Smith & Parker 1976; Parker & Rubenstein 1981). This prediction is important in all of these studies as it provides a basis from which we might determine what is important to salticid males. However, it is critical that we ask the right questions.

Although two of the three salticid species studied, *E. parvula* (Chapter 2) and *P. fimbriata* (this chapter), escalated the level reached in male-male conflict during lure tests, the third species (*J. queenslandicus*) did not. Why this species might be different is not known, but possibly *J. queenslandicus* relies on a different sensory modality for detecting females.

Wells (1988) found a similar increase in the level to which intrasexual conflict escalated in the presence of optical cues from an adult conspecific female in his study of male-male conflict in *E. parvula*. Wells (1988) interpreted this increase in escalation as evidence of competition by males for a resource where the resource was conspecific females.

However, there were potentially important, but uncontrolled, variables in Wells' (1988) experiment, leaving at least two alternate hypotheses that might account for his findings. The experimental tests were not started until the males were courting the female (i.e., the divider was not removed and the spiders could not interact until both spiders were courting the lure). This was done to ensure that the males had actually seen the lure and recognised it as a conspecific female. Salticid-eye fovea have narrow fields of view and the eyes tubes do not always point straight-ahead (Land 1969a; Land 1969b; Blest et al 1990; Harland & Jackson 2000). Therefore, one cannot be sure that an image of the lure is falling on the fovea simply because the spider has its front end oriented towards the lure. Even if an image is projected onto the fovea, the salticid has to attend to the image. People can look straight at things and not really see what is in front of them. A salticid might be subject to the same lapses. During the control tests, each test was started when both spiders were oriented towards the moving (bare) cork. This was unavoidable, as getting the males to court a bare cork was not feasible. However, this does leave a possible alternative which might explain the results obtained. Two alternative hypotheses are presented below:

Hypothesis 1) Once a male begins courting, the performance of courtship changes the male's internal state in such a way that the male becomes more likely to escalate male-male conflict to a higher level than would normally occur. The idea is that, if the male is already in 'display mode', then maybe there is something like an inertia that carries over into male-male display.

From what we know about the test spiders' behaviour in Experiment 3 of Chapter 2 and in this chapter, hypothesis 1 may not be likely. When the divider was removed to initiate experiments, most spiders continued to court the lure or else turned away briefly but then resumed courting the lure. Consistent with hypothesis 1, this might be interpreted as the display threshold having been lowered and the 'inertia' created by the act of courtship providing impetus to continue displaying. Possibly if the spiders had not been displaying when the divider was

removed they would have reacted quite differently, say, by fleeing rapidly. However, once males initiated intrasexual displaying they continued displaying this way until one male fled. If the act of performing courtship displays lowers a male's threshold to perform other displays, as hypothesis 1 suggests, then male-male display would be expected to be lower the threshold to perform courtship displays. There might be a feedback effect where the act of courtship lowers the threshold to perform intrasexual display, and in turn lowers the threshold to perform courtship displays. If hypothesis 1 were true, then we would expect to see the two spiders alternate between courtship and male-male displays in the above experiments (i.e., Experiment 2 of Chapter 3 and this chapter). Possibly, it is only the act of performing courtship displays that lowers the threshold to perform other displays. If this is the case, then this suggests that courtship displays should be important enough to interrupt male-male conflict. That males switch solely to intrasexual displays may be seen as evidence against Hypothesis 1. However, during male-male display the rival male displayed in return, but the lure did not respond to the males courtship display. This may give male-male display extra precedence over courtship display. At this time we cannot rule out hypothesis 1.

An interesting prediction from this hypothesis appears to be implied. If an experiment similar to the one above (i.e., Experiment 3 in Chapter 2) was performed, but removing the lure from the arena simultaneously with removing the divider, then there should be no increase in aggression as the males will have stopped displaying. If what primes the male is its prior behaviour (courting a lure), then the removal of the lure during the time when the two males interact should not make much difference, as the threshold that inhibits displaying (of any kind) has been lowered. Prediction: males still escalate intrasexual selection.

An array of additional hypotheses could be formulated and tested should this prediction hold. The possibility that it is specifically prior performance of courtship behaviour that primes males to escalate in male-male conflict could be explored. This would make the most direct sense in relation to the hypothesis that intrasexual selection has driven the evolution of a conditional strategy in male-male conflict. Alternatively, it might be that other activities at the time when the barrier is lifted will prime males to escalate in male-male conflict. For example, if two males had been performing threat displays at a lure made from a conspecific male prior to lifting the barrier, would they have escalated compared to what they would have done in the control? Another experiment could test the effect on intrasexual conflict of having two males stalking a lure made from a fly just before the barrier is lifted.

The alternative hypothesis considered here might be seen as something akin to the general-agitation hypothesis. Males engaged in activities other than courtship might tend to escalate when another male appears (i.e., when the barrier is removed). If this is so, then it is not going to be as clear that the hypothesis related to intrasexual selection is implied. Even if general agitation from activities other than courtship is important, courtship might have an added effect. An added effect would be supportive of the intrasexual-selection hypothesis, but at the same time acknowledge that more than this is involved. General agitation might turn into something more complicated than simply an all-or-none effect. It might be that different activities have different levels of effect. Testing all of these possibilities was beyond the scope of this study.

Hypothesis 2) Salticid males escalate male-male conflicts when they see a conspecific female during the time (or just before the time) when they see each other. This hypothesis implies a different process going on in the male. This is more of a cognitive hypothesis. The idea is that males escalate because they 'know' a female is in the area.

These hypotheses may appear to state the same thing, but they are not identical. The male must be aware of the female, in some sense, to initiate courting. However, hypothesis 2 postulates awareness of a type that implies an internal process applies (i.e., that some cognitive process in a different sense, is occurring). Stimulus (optical cues

from female) followed by response (courtship) may be more or less an automatic function and is what hypothesis 1 pertains to. A cognitive process would imply something in between the stimulus and response steps of the behaviour. In other words, the stimulus is followed by awareness of what the stimulus is a cue for. Hypothesis 2 proposes that this state of awareness is what influences male behaviour.

We could envisage awareness being held in memory somewhere. The activity of courting might itself be called memory, but not in the same way. How a lure made from a female affects escalation of male-male conflict, likewise, can be envisaged as an 'online' or 'offline' process. 'Online': stimulus (optical cues from females) followed by response (courtship) followed by courtship performance itself pushing male-male conflict to higher level. 'Offline': stimulus (optical cues from females) followed by awareness (a cognitive state) held in memory and influencing reaction to next stimulus (optical cues from males).

Testing Hypothesis 2 would seem to require experiments where males can be made aware of a female's presence without causing them to start courting. This would be difficult to do with optical cues, but might be made more feasible by switching to testing with olfactory cues. Therefore, experiments were designed that could explore the effect of olfactory cues from conspecific females on salticid male-male conflict.

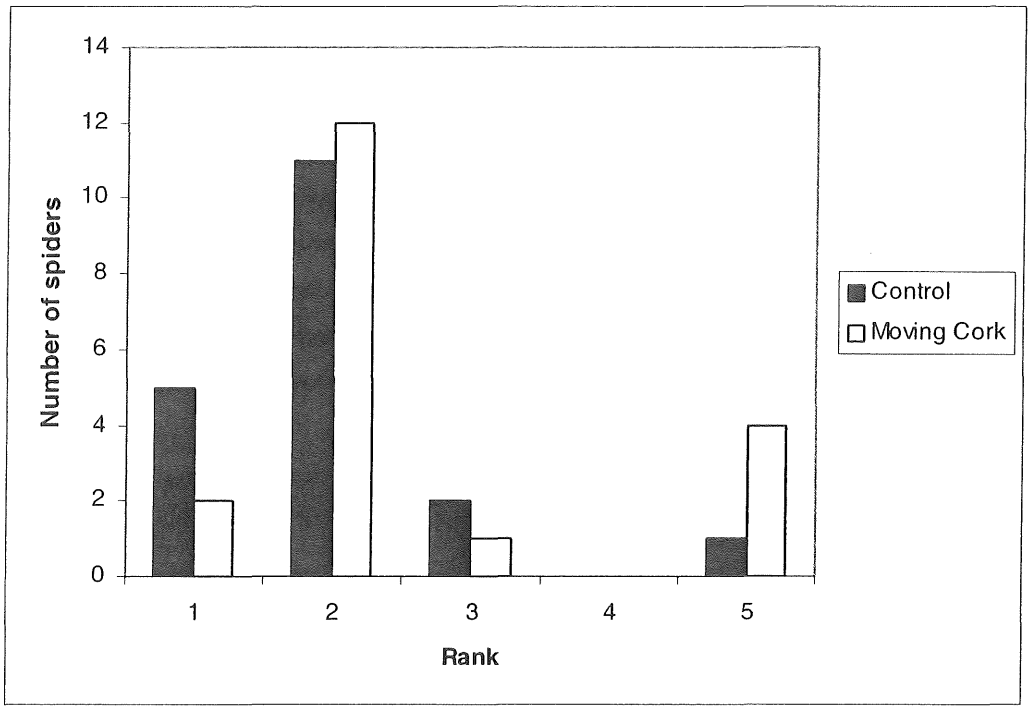

Fig. 14: Number of contests (N=20) of *Portia fimbriata* males at each level of escalation with lure (made from a conspecific female) present and absent.

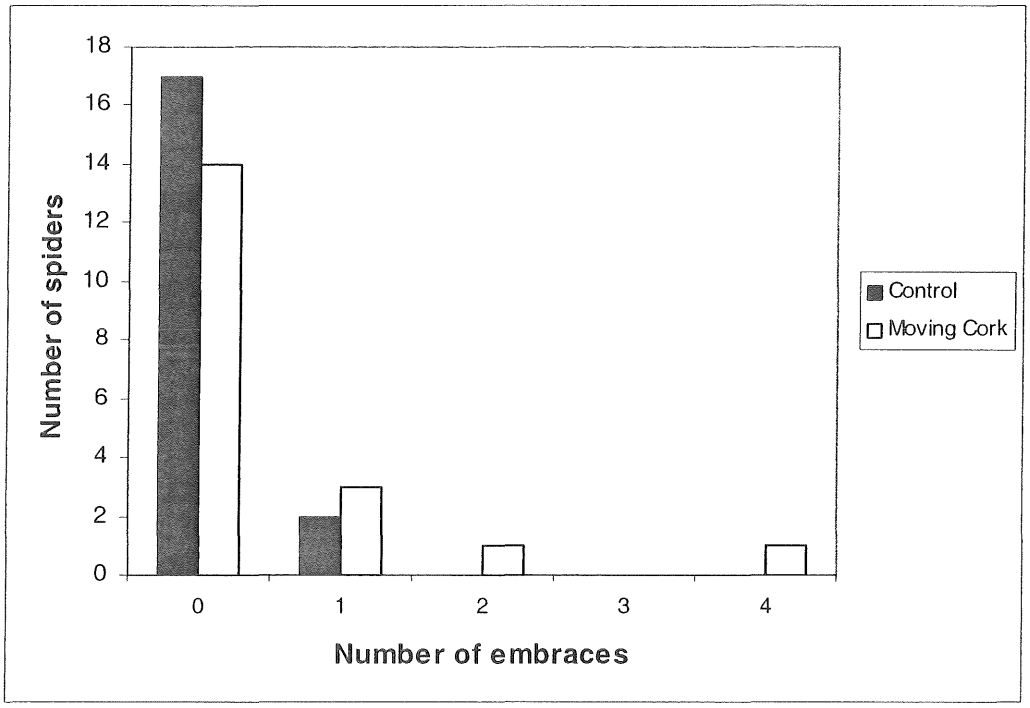

Fig. 15: Number of embraces by *Portia fimbriata* males in each contest (N=20) with lure (made from a conspecific female) present and absent.

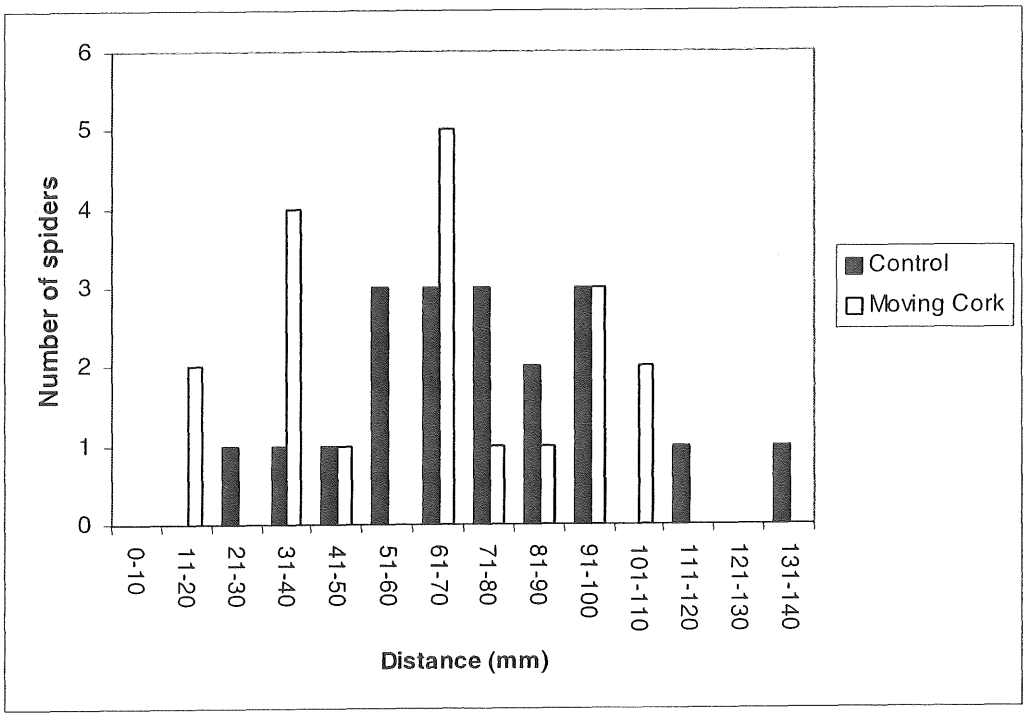

Fig. 16: Comparison of the distance at which pairs of *Portia fimbriata* males first displayed with lure (made from a conspecific female) present and absent (N=20).

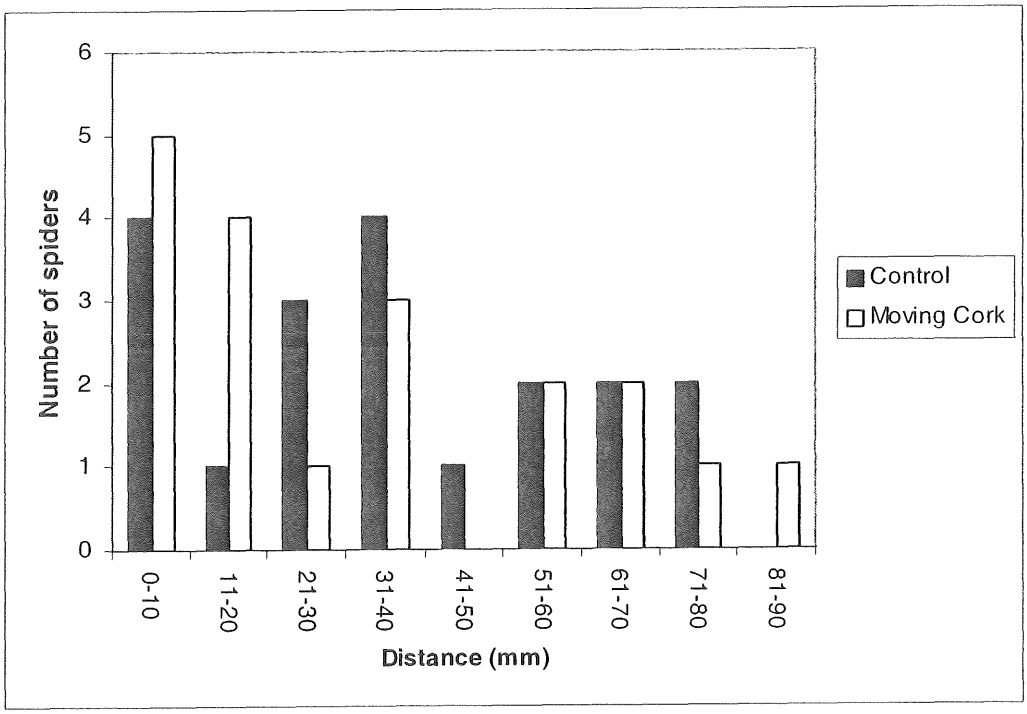

Fig. 17: Comparison of the distance to which pairs of *Portia fimbriata* males closed in tests with lure (made from a conspecific female) present and absent (N=20).

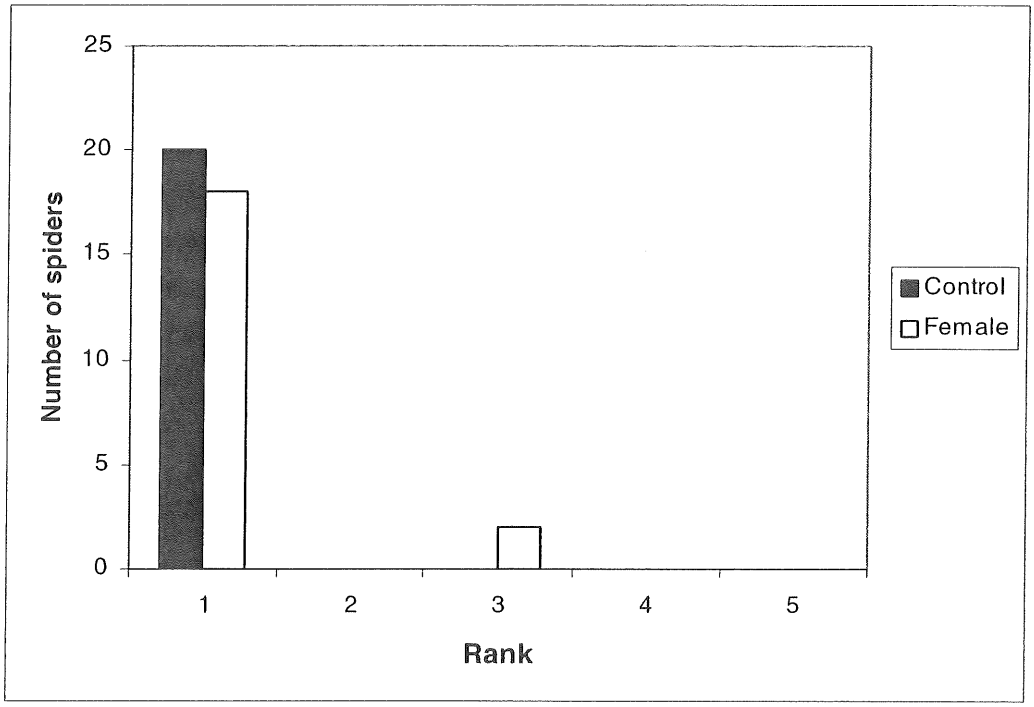

Fig. 18: Number of contests (N=20) between *Jacksonoides queenslandicus* males at each level of escalation with lure (made from a conspecific female) present and absent.

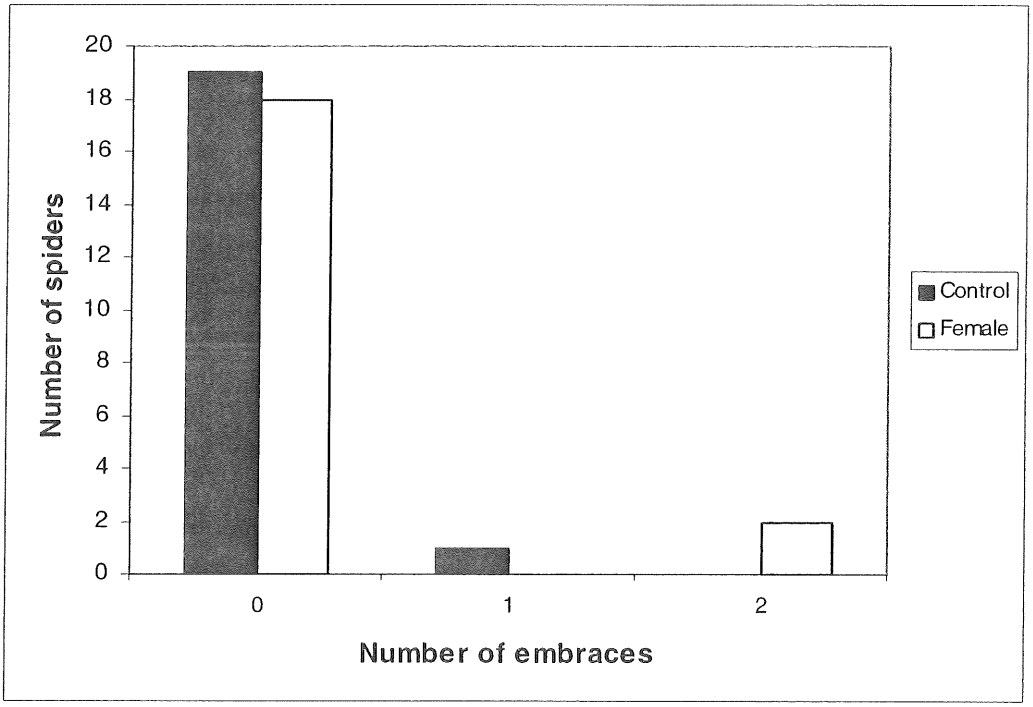

Fig. 19: Number of embraces in each contest (N=20) with lure (made from a conspecific female) present and absent between *Jacksonoides queenslandicus* males.

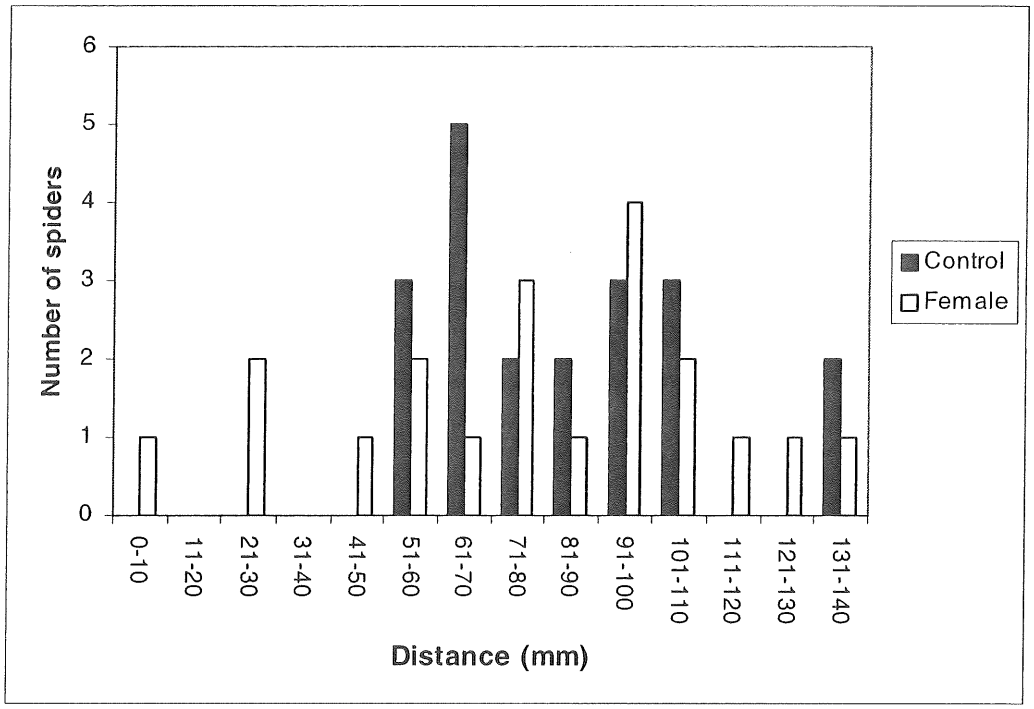

Fig. 20: Comparison of the distance at which pairs of *Jacksonoides queenslandicus* males first displayed with lure (made from a conspecific female) present and absent (N=20).

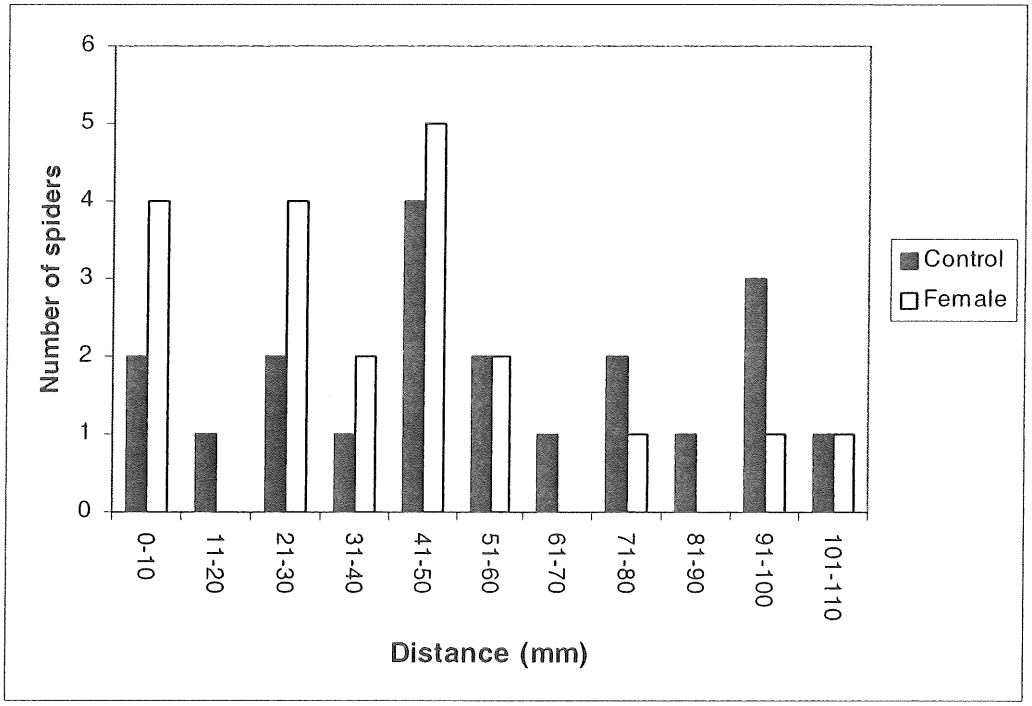

Fig. 21: Comparison of the distance to which pairs of *Jacksonoides queenslandicus* males closed in tests with lure (made from a conspecific female) present and absent (N=20).

Chapter 4: Influence of optical cues on female-female conflict in *Portia fimbriata.*

INTRODUCTION

With almost 5,000 described species (Coddington and Levi 1991; Zabka 1993), the Salticidae is the largest spider family. Being well known for their visual acuity and visual capabilities, these spiders have visual capabilities with no equal among animals of comparable size (Land 1969a,b; Blest et al. 1990; Jackson & Harland 1998; Harland et al. 1999). Salticids are diurnal, cursorial predators that use vision to guide predatory sequences when hunting a variety of insects and other arthropods (Forster 1982a; Jackson & Pollard 1996; Harland & Jackson 2000).

It is of no surprise that vision plays a large part in salticid communication. Visual displays are used by salticids to communicate by using a variety of body postures and displays (Jackson 1982a). These displays are typically split into two categories: courtship and intrasexual displays. If an adult male salticid encounters a conspecific female, the resulting displays are usually called 'courtship' (Richman & Jackson 1992). The male seems to be trying to persuade the conspecific female to mate with it (Richman 1982; Jackson & Pollard 1997). There is evidence, although limited, that females choose the particular males with which they mate on the basis of their display (Jackson 1982b; Jackson & Pollard 1997).

When two salticids of the same sex meet, they usually perform threat display that appears 'aggressive' even to a human observer. For example, when *Portia fimbriata* males meet they adopt a posture with legs flexed and held out to the side, the chelicerae is held open and the fangs are extended (Jackson & Pollard 1997). Jackson and Pollard (1997) note that this posture (called 'hunched legs') appears similar to the posture adopted immediately prior to prey capture, and may possibly have evolved as a type of sensory exploitation. Male-male aggression is much more pronounced than female-female aggression in most species of salticids (Chapter 2), but the reasons underlying the greater development of male intrasexual conflict are poorly understood.

Findings of Chapter 2 and 3 suggest that male-male conflict in salticids may often be governed by a conditional strategy (Chapters 2,3). In a species with a conditional strategy, each individual has a set of tactics. Each tactic deals with a certain situation (e.g. courtship, intrasexual competition, or predation). Which particular tactic is used depends on a set of decision rules that specify when to use each tactic (Dominey 1984). Conditional strategies are of interest because they potentially reveal specific selection factors that have shaped the evolution of particular behaviour patterns (see Alcock 1998). Studying the rules governing conditional strategies can be envisaged as asking an animal, in experiments, what resources matter to it.

Conditional strategies appear to be common in salticids where they govern many aspects of mating (Jackson 1977, 1982b) and predatory behaviour (1992a). It appears that male salticids may also have a conditional-strategy rule that is employed during intrasexual conflict: when a conspecific female is detected, escalate male-male conflict to a higher level than would be reached if a female was not present (i.e., change from 'display at a low level of risk to self' to 'display at a high level of risk to self'). However, the adaptive reasons underlying this rule are not clear. One possibility is that sexual selection is acting on male-male conflict in salticids. Recent findings (Wells 1988; Chapters 2,3) from testing pairs of salticid males have shown an increase in the level reached in male-male conflict in the presence of a female compared with the absence of a female. Three species were tested, *Euophrys parvula*, *Jacksonoides queenslandicus* and *Portia fimbriata*. Pairs of males were tested in the presence and absence of optical cues from a lure made from a conspecific female. *E. parvula* and *P. fimbriata* males more often escalated competitions from visual displays into physical contact when the lure was present than when the lure was absent. It appears from these studies that the decision rule could be stated: when a conspecific female is detected, escalate

male–male conflict to a higher level (change from 'display at a low level of risk to self' to 'display at a high level of risk to self') than would be reached if a conspecific female were not present. Wells (1988) suggested that these salticids are fighting to obtain a particular resource (i.e., a conspecific female), and the specificity of the rule would be difficult to explain unless conspecific females are, as hypothesised, a resource that has shaped male-male display behaviour. However, that the rule is this specific needs to be verified with experimental evidence.

Recent studies (Wells 1988; Chapter 2, 3) suggest that salticid males have evolved under intrasexual selection pressure to compete directly with one another, using visual displays and physical contests, for access to mates. A prediction from this hypothesis is that more pronounced aggression in male-male conflict will occur in males than females.

This is because in spiders, as in most animals, including spiders, parental investment is greater in females than in males (Trivers 1972), a disparity that stems from how gamete size differs between the sexes. Males tend to produce many small gametes whereas females usually produce a few large gametes (Krebs & Davies 1993). A consequence of this disparity is that females tend to be a severely limiting resource for males (Ryan 1997). The sex that supplies more investment to the next generation is expected to be choosier during mate selection, as this sex has more to lose if a poor quality mate is chosen (Krebs & Davies 1993). A possible consequence of female mate choice is that a few males will have disproportionately large reproductive success (Ligon 1999).

However, males competing for access to females does not occur in all species and cases of sex-role reversal, where females compete for mating opportunities with specific males, are known in species where males provide more reproductive investment than females (e.g., in some insects (Thornhill & Alcock 1983) and birds (Ligon 1999)). One example of males providing more parental investment than females is in the Mormon cricket, *Antabrus simplex* (see Thornhill & Alcock 1983). The male Mormon cricket supplies the female with a protein meal in addition to sperm by means of a spermatophore during copulation. The spermatophore of the Mormon cricket can be up to 25% of a male's body weight and is very costly to produce, which means it limits the number of times a male can reproduce. Consequently, it is the male Mormon cricket that is selective about mate choice, and females fight among themselves for access to males.

In *Portia fimbriata*, the pattern of female-female conflict is unusual. Unlike most species of salticids it is particularly ferocious, being more pronounced than intrasexual conflict in males (Jackson & Pollard 1997). From what we know about biology, it seems unlikely that female-female competition is driven by intrasexual selection pressure. In all spider species, including salticids and including *P. fimbriata*, the female provides the majority of the parental investment (Foelix 1996). A female spider must supply her offspring with all the energy and nutrients required to develop and grow until the second instar spiderling captures its first prey. In contrast, male spiders contribute only genetic material to the next generation. In fact, males often die soon after copulation (Foelix 1996). That is, there appears to be little likelihood of sex-role reversal in *P. fimbriata* females.

If *P. fimbriata* females, like all female spiders, supply most of the parental investment, then why is female-female aggression so pronounced in this species? In some instances, conflict entails a female *P. fimbriata* protecting her nest and eggs from a conspecific female attempting to eat the eggs and take over the web as her own oviposition site (Clark & Jackson 1994b), but this may not always be the case. The reasons, underlying the extreme intrasexual conflict of *P. fimbriata* female remains unresolved.

Part of the rationale behind the set of experiments in the present chapter is to see *P. fimbriata* females adopt a conditional conflict strategy. More specifically, do *P. fimbriata* females escalate intrasexual conflict in the presence of optical cues from a conspecific male? By looking for this particular conditional strategy we are effectively asking whether role reversal goes further than simply aggressive intrasexual conflict. Is the intense

female-female conflict seen in *P. fimbriata* partly an evolutionary product of females fighting from males?

An experiment from Chapter 3 tested male-male conflict in *P. fimbriata*. This experiment showed an escalation of male-male conflict in intrasexual contests when a lure made from a conspecific female was present compared with when no lure was present. The hypothesis Wells (1988) suggested to explain this escalation was that intrasexual conflict escalates because males somehow perceive the presence of a conspecific female (that they deliberately escalate intrasexual conflict as a means of obtaining this particular resource, as game theory predicts) (Wells 1988). However, an alternative hypothesis for results that has not been ruled out can be stated as follows: escalation of male-male conflict after detecting a conspecific female is part of a generalised phenomenon in salticid intrasexual conflict and not a result of detecting a female per se. The idea behind this hypothesis is that the female is part of a larger category of objects that cause escalation. This larger category may include all conspecifics, prey and predatory species of these salticids. In Chapter 2, movement alone (in the absence of any other cues) was shown to affect the level to which intrasexual conflict behaviour of a New Zealand salticid, *E. parvula*, escalated. This suggested as an alternative to Wells' (1988) hypothesis that male-male conflict has nothing in particular to do with intrasexual selection, but instead can be interpreted as a consequence of general agitation.

One way of testing hypotheses is to systematically change the lure used. Another way is to examine the effect of a lure made from a conspecific male on female-female conflict in salticids. If the escalation of intrasexual conflict in salticids can be explained as some sort of general agitation, then escalation of female-female conflict is expected in the presence of a conspecific male. However, if the escalation seen in *P. fimbriata* males (Chapter 3) is related strongly to intrasexual selection then females would not be expected to be as prone as males to escalate when tested in a similar way.

For the objectives of this chapter, *Portia fimbriata* provides several advantages over the other two species of salticid (*E. parvula* and *J. queenslandicus*) tested in Chapter 3. Female-female conflict is particularly pronounced *P. fimbriata*, unlike in most salticids (Jackson 1986a; Jackson & Willey 1995). *P. fimbriata* females exhibit the whole range of possible displays over a series of tests, from visual displays to physical contact, whereas females from other species tend to perform only visual displays during female-female conflict (Jackson & Pollard 1997). This means that escalation should be easier to detect in *P. fimbriata* females (if it occurs). Another advantage is that this species is slow moving compared with the other two species of salticid. This slow moving nature probably has its roots in *P. fimbriata*'s araneophagic lifestyle. Queensland *Portia fimbriata* hunt salticids and have several adaptations in dealing with these potentially dangerous prey, one such adaptation is a slow and choppy walking gait (Jackson & Blest 1982; Jackson & Pollard 1996). This has a practical advantage in handling *P. fimbriata*, as *P. fimbriata* are less flighty than the females of the other two species. During the intrasexual conflict tests in Chapter 2 and 3, several tests had to be aborted because the spiders appeared unduly disturbed (running wildly around the arena) during removal of the opaque, cardboard divider that separated the spiders prior to testing (see below for full description). It was judged that subsequent behaviour following this kind of wild decamping would probably not be normal. Although not tested statistically, wild decamping seemed to happen less in tests using male *P. fimbriata* than in tests using *E. parvula* and *J. queenslandicus* males. Yet another advantage is the large body of work that has been done on the behaviour of *P. fimbriata* (see reviews in Jackson & Pollard 1996, 1997; Harland & Jackson 2000). Much is known about the capabilities of *P. fimbriata*, aiding the making of predictions about how these animals may behave.

MATERIALS AND METHODS

General

All spiders tested were adults from laboratory cultures established by collecting from the tropical rainforests in the vicinity of Cairns, North Queensland, Australia. Standard rearing and maintenance procedures were used in a controlled-environment laboratory. Lights came on at 0800h and went off at 2000h. For more details see Jackson & Hallas (1986). All testing occurred between 0900h and 1500h. Because female-female conflict tests were in basic respects the same as described elsewhere (Chapter 2), only essential details will be provided plus information about the display behaviour of female *P. fimbriata*. The rationale for ranking levels of intensity reached in female-female interactions was as in Chapter 2, Chapter 3 and Wells (1988).

Description of displays and ranking

Only brief descriptions of intrasexual behaviour are given here, but details for both species can be found elsewhere (Jackson & Hallas 1986). Rankings are listed from lowest intensity to highest intensity.

1. Posturing with legs hunched (rank 1). The first three pairs of legs were brought forward, flexed and held close to the body. Adoption of this posture, which was called the 'hunch display', was usually performed while the two males were distant from each other, and was typically the display first adopted when a female encountered another conspecific female. However, hunch display was not exclusive to early in encounters, but instead tended to be the dominant display throughout the interaction whenever spiders were at least 10 mm apart.
2. Posturing with legs erect (rank 1) while no more than 10 mm from the other male (rank 2). The first pair of legs alone, or more often the first two pairs of legs together, were held out stiffly above the substrate at about 45° to the horizontal and were angled between 45-90° out to the side of the males' body. This display was often used briefly at a distance greater than 10 mm in conjunction with the hunch posture, but at this distance it did not qualify as rank 2. While 10 mm or less, from each other, this posture (called 'erect display') tended to be maintained for prolonged periods, during which time the two spiders usually manoeuvred around each other actively.
3. Embrace (rank 3). The spiders brought the front of their cephalothoraces together and pushed against each other. As the spiders approached the erect legs of the two spiders displaying overlapped as they got closer. The cephalothoraces of the two spiders were often raised, with the abdomen tilted down. These displays only lasted 5-10 s.
4. Grapple (rank 4). Embracing spiders grappled by moving their overlapping forelegs forward over the opponents' forelegs and forcefully flexing these legs. This display sometimes pulled off one of the opponent's legs.
5. Fight (rank 5). While embracing one female occasionally pushed the other female over onto its dorsal surface. Usually, the up-ended spider righted itself and ran away. However, a fight occurred if the rival spider walked over the up-ended spider. The pair fought by grappling wildly until one male ran away several seconds later. While fighting, the spiders were venter-to-venter.

Basic experimental procedure

Encounters between two adult conspecific males were staged the test arena used in previous experiments

(experiments 2 and 3 of Chapter 2, Chapter 3) (Fig. 1). These male-male encounters were of a paired-test design with each spider tested in the presence and in the absence of optical cues from a lure made from an adult conspecific female.

In this experiment lures were made from adult *P. fimbriata* males that had been asphyxiated with CO_2, soaked in ethanol, dried and mounted in a lifelike posture and then freeze-dried. The freeze-dried lure was glued to a cork (25 mm at the widest point, 20 mm at the finest point and 40 mm high) and coated with an aerosol plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty).

The spiders were only tested once within a single 24-h period. No spiders were tested more than twice.

The females were put on either side of the opaque cardboard divider that split the test arena into two. This divider was placed so that the lure was visible to the two test spiders, but still obscured the spiders from each other. During the experimental tests the lure was moved until both test spiders were courting the lure. When both spiders were courting the lure, the divider was removed. Removing the divider allowed the test spiders to interact.

The control test was conducted in a similar way, except that only a bare cork (25 mm at the widest point, 20 mm at the finest point and 40 mm high) was present instead of a lure. The cork was moved until both spiders had turned so that their anterio-median eyes were oriented toward the cork. The spiders were not required to court the bare cork. Once both spiders were facing the cork the divider was removed.

Similar to Chapter 3, the general-agitation effect was not tested for *P. fimbriata* females (i.e., the equivalent of Experiment 1 in Chapter 2 was not conducted), the possibility of this effect was controlled by having movement occur in both the control (bare cork) and the experimental (cork plus lure) tests.

A test started when the two spiders first exchanged displays. If both spiders had not displayed within 30 min after the divider was removed, the test was aborted. The test ended when one spider retreated and did not return or the spiders lost interest in each other (definition: both spiders stopped displaying and either wandered away or became quiescent).

The details about interactions (the number of times the spiders embraced, the distance between the spiders when they first displayed and how close the spiders came to each other during a test) were recorded verbally on audiotape and later transcribed. Also recorded was the maximum rank of the loser (i.e. the spider that decamped first and did not return) of a contest. This determined the level of escalation of a given conflict and enabled comparison between the control and experimental tests.

Appropriate statistics for pair-wise data were used (e.g., McNemar tests for significance of changes & Wilcoxon tests for paired comparisons: Sokal & Rohlf 1995). The P-values given are after Bonferroni adjustments whenever the same data are used for multiple comparisons (Rice 1993).

RESULTS

When the divider was removed, the *P. fimbriata* usually responded by turning toward this movement caused by the divider. The spiders reacted slowly and often the divider was completely removed before the spiders had finished turning. One spider reacted to the other spider that might be moving around the arena or sitting quiescent. Often the female that reacted to the other spider started to stalk the other female instead of initiating courtship. In these instances, the first female slowly stalked the second spider. If the second spider did not turn towards the first, the first spider attempted to leap on the second spider. Three spiders were killed when this happened during experiments (data for these were not included in the data set). Sometimes the first spider was not successful at capturing the second because it leapt on but did not kill the second spider or the second spider reacted to the first spider approaching and started to display itself, more or less, simultaneously. The hunched display was usually the first to

be used. Spiders sometimes interspersed hunched displaying with the erect legs displaying. The spiders would often get close to within 10-20 mm of each other and slowly manoeuvred around each other displaying with erect legs. Interactions were highly variable in length, sometimes taking only a few minutes and in other interactions lasting for nearly an hour, and in a few instances lasted more than an hour. When females escalated to physical contact they often embraced then backed away while displaying with hunched or erect legs and then moved back together and embraced again. This pattern of embracing then using visual displays before embracing again could occur several times during a single interaction.

There was no significant difference in the level of escalation reached in the control and the experimental (male lure present tests) (Fig. 22). During tests with a bare cork, the median rank reached was rank 1. However, in tests with a lure made from a conspecific male, the median rank reached was 3. Even though females appeared to escalate to physical displays more often when the male lure was present, this was not significantly different from the control tests (Wilcoxon signed rank test, 2 tailed, P=0.23, N=20). Nor did the number of embraces vary significantly (Wilcoxon signed rank test, 2 tailed, P=0.82, N=20) between tests (Fig. 23). The median number of embraces in both the control tests and lure tests was 1. There was no significant difference in the distance at which the females first displayed (Wilcoxon signed rank test, 2 tailed, P=0.25, N=20). Spiders initiated display at a median distance of 59 mm during control tests, and first displayed at a median distance of 71 mm during experimental tests (Fig. 24). The distance to which the spiders closed during interactions did not differ significantly between tests (Wilcoxon signed rank test, 2 tailed, P=1.0, N=20). During control tests males approached to a median distance of 18 mm, when visual cues from a conspecific female were present, males approached to a median distance of 19 mm (Fig. 25).

DISCUSSION

The hypothesis considered here can be envisaged as a refined version of the general-agitation hypothesis (Chapter 2). In the general-agitation hypothesis in chapter 2, the extraneous stimulus was movement, while in this finer-grained version, the stimulus was the presence of a conspecific (of any sex). The idea is that agitation increases the level to which intrasexual conflict escalates by making the interacting spiders more aware of stimulus, and by causing an increase in escalation in intrasexual competition as the spiders become aware of each other sooner. Agitation, if it is a background phenomenon should affect female-female conflict, as well as male-male conflict, and cause escalation. *Portia fimbriata* females, that exhibit such fierce intrasexual conflict, might be thought to be especially prone to any such agitation effect. However, no escalation in aggression was detected in the presence of a conspecific compared with its absence.

Why optical cues from a lure made from a conspecific of the opposite sex affected male-male but not female-female interactions is not clear. In Chapter 2, it was argued that agitation effects from movement (Chapter2) might be consistent with intrasexual sexual selection hypothesis. The agitation effect might work by alerting a male to the possible presence of a female, but with the level of certainty, about whether the possible female really being a female very low. There is no evidence to support a comparable hypothesis for female in the presence of a possible male.

Another interpretation discussed in Chapter 2 was that the agitation effect works by alerting the male to the presence of a potential resource, but where the exact type of resource is not determined, be it prey, mate, predator or whatever. The idea is that by becoming more alert, and as a consequence more 'aggressive'; the male can take advantage of the presence of an unspecified resource. This hypothesis, however, would not appear applicable to female as well as male. Some resources, especially food, would be more relevant to females than to males. It seems

sensible to think that if this agitation effect works for males it should also work for females. It is tempting from this information to conclude that it must be intrasexual selection driving this agitation effect

However, there are complications. As females do not initiate courtship, it had to be assumed that the *P. fimbriata* female had seen the lure, and recognised it as a conspecific male, simply when they had oriented towards it. This assumption is questionable. As discussed earlier, salticids can be facing towards an object yet looking elsewhere.

If females did see the lure and did perceive it as a conspecific male then this could tentatively be seen as support for the hypothesis that male-male conflict behaviour in salticids has evolved under intrasexual selection pressure. Wells (1988), using a game theory model, first tested this idea. The prediction Wells (1988) was testing was that males would tend to escalate during intrasexual conflict to more dangerous levels of interaction when a conspecific female was present (see: Maynard Smith & Parker 1976, Parker & Rubenstein 1981; Maynard Smith 1982). Wells (1988) assumed that conspecific females were the resource for which *Euophrys parvula* males competed and this assumption appeared to be correct. Wells (1988) reported a significant degree of escalation in male-male conflict in the presence of visual cues from a conspecific female compared with in the absence of these cues. However, Wells' (1988) results could also be attributed to movement in the environment causing the salticids somehow to become more 'alert' and 'agitated'. Experiments in Chapter 2 showed this is a viable alternative. However, when Wells' (1988) experiment was repeated but with controls for the effect of movement, his results were duplicated for *E. parvula* males, and also for *P. fimbriata* males.

Sexual selection theory suggests that, for the majority of species, males compete more for females than vice versa (Trivers 1972; Gould & Gould 1989; Andersson 1994). Possibly the findings in Chapter 2 and 3 are another example of males fighting for access to females. These results might be seen as consistent with the widespread pattern of females not fighting for access to males. However, even with improved methods, the conclusion that intrasexual selection has driven the evolution of male-male conflict behaviour in jumping spiders is questionable. The aim of this set of experiments was to narrow down one of the alternative hypotheses. Not finding evidence that female-female conflict escalates in the presence of a conspecific male is consistent with the hypothesis that male-male conflict in salticids has evolved under intrasexual selection, but strong support is still lacking.

Another possible reason for the difference found between male and female intrasexual conflict could be slight differences in the methods used in the experiments using *P. fimbriata* males and *P. fimbriata* females. This is a consequence of the courtship behaviour of female salticids. Female salticids normally perform few, if any, displays during courtship, relying instead on the male to display to the female (Jackson 1982a). Females are thought to select a mate on that basis of these displays (Jackson 1982b; Jackson & Pollard 1997). *Portia fimbriata* females do display during courtship, but usually only in response to a *P. fimbriata* male that initiated the interaction (Jackson & Hallas 1986; Jackson & Pollard 1997). When testing the effect of female lures made from a conspecific on male-male conflict in *P. fimbriata,* it was certain that the males saw the female. This was because a condition of the experiment was such that the males had to be courting the lure before the two spiders were allowed to interact. Because of this, it was certain that the spiders had seen the lure and, more importantly, had recognised it as a conspecific female. This can be concluded because males perform courtship displays only to conspecific females. As females do not initiate courtship we could not use this method. For this reason the divider was removed once both spiders were oriented towards the lure (similar to the control).

Having males court the lure before allowing them to react was not without its own inherent problems. Possibly the act of courtship somehow primes males to escalate male-male conflict by lowering the threshold to

perform displays. In other words, the spiders might display harder (i.e., they might escalate to higher ranked behaviour) during male-male conflict because they have recently been using courtship displays.

This seems to be an inherent problem with using visual cues in this type of test. When testing females, one cannot be sure a salticid is seeing and/or recognising a lure. When testing males one can be sure the male is seeing a female lure, but one cannot be sure that the act of displaying itself is not in altering the male's subsequent behaviour. Also the reactions of males and female salticids cannot be reliably compared, as different methods were used.

Possibly the answer to these problems is to test these salticids using cues from conspecifics of the opposite sex that are not optical cues. Salticids are known to use chemotactile, olfactory (Pollard et al 1987; Jackson 1987; Clark et al in press) and vibratory cues (Edwards 1981) in predatory and courtship sequences. Therefore, cues in one or more of these modalities might be substituted successfully for visual cues. A sensory modality is needed that permits confidence that the cue is being detected but without special requirements, such as courtship displays, to ensure that the cue has been received. Olfactory cues may be the most suitable candidate for this. In future experiments, I investigate whether olfactory cues from conspecifics of the opposite sex affect intrasexual behaviour in salticids.

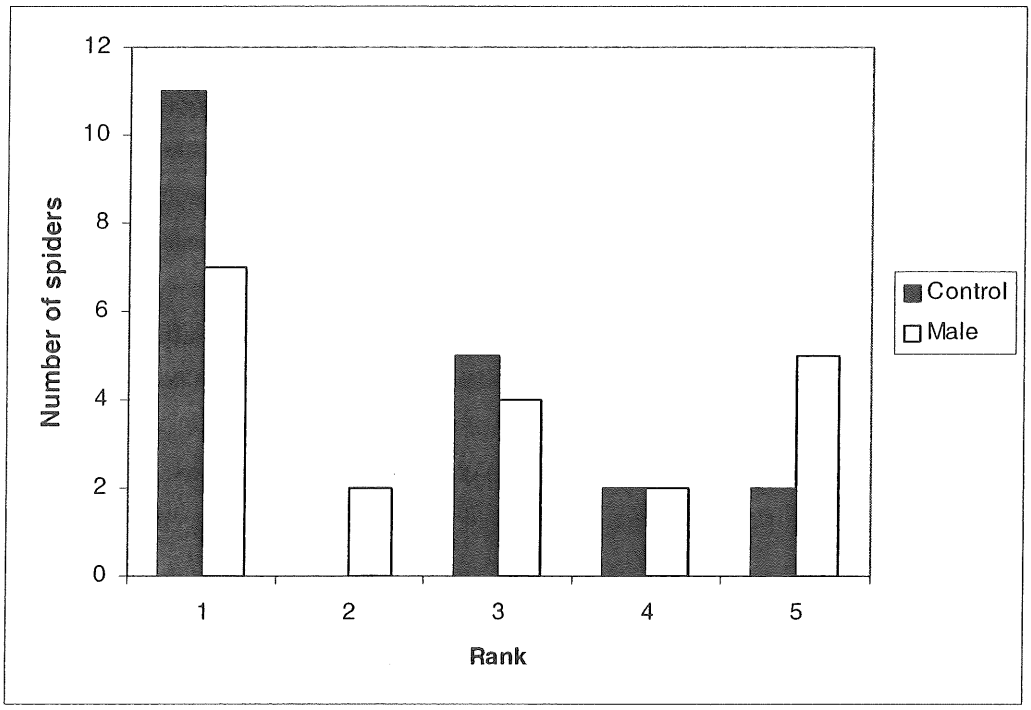

Fig. 22: Number of contests (N=20) at each level of escalation with male lure present and absent. Contests between *Portia fimbriata* females.

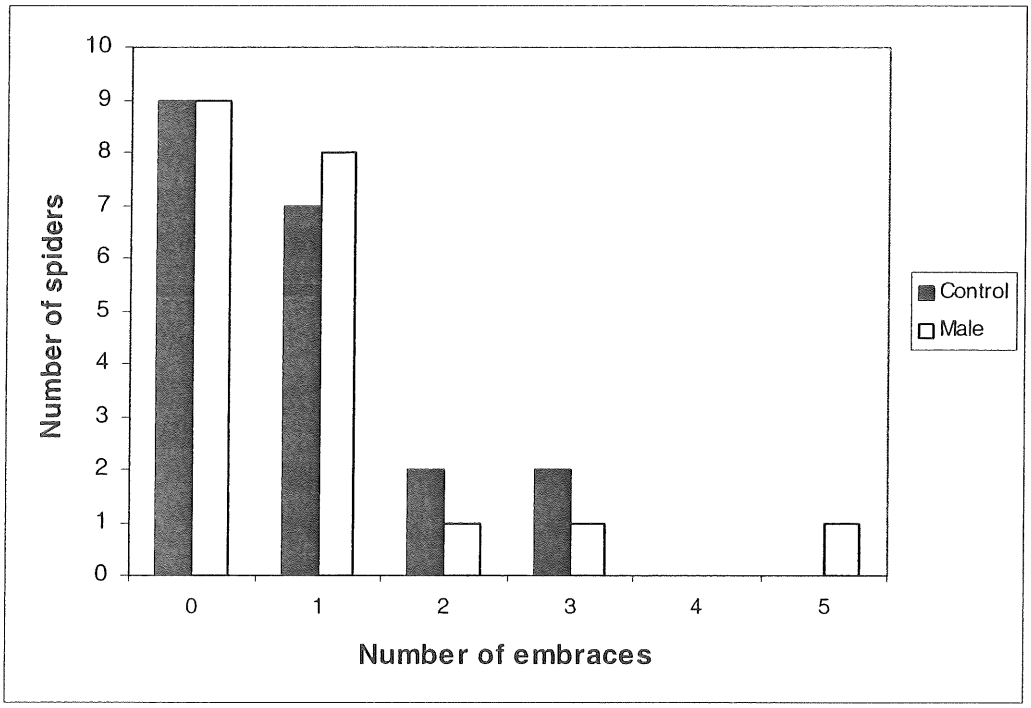

Fig. 23: Number of embraces in each contest (N=20) with male lure present and absent. Contests between *Portia fimbriata* females.

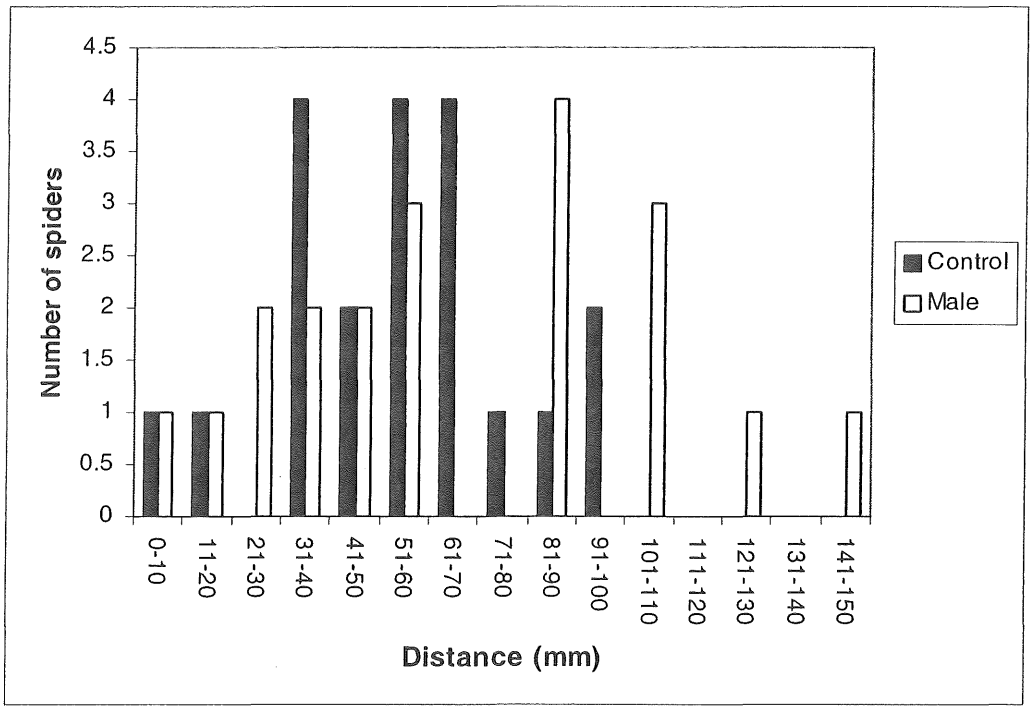

Fig. 24: Comparison of the distance at which pairs of *Portia fimbriata* females first display with male lure present and absent (N=20).

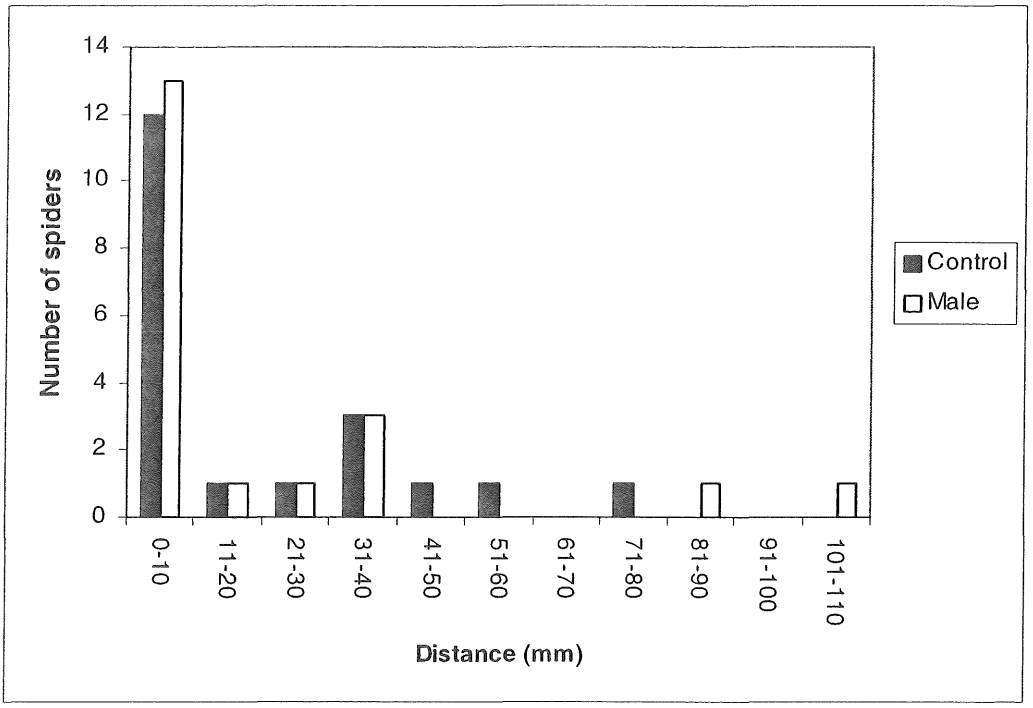

Fig. 25: Comparison of the distance to which pairs of *Portia fimbriata* females close in tests with male lure present and absent (N=20).

Chapter 5: Influence of olfactory cues on male-male conflict in salticids.

INTRODUCTION

Jumping spiders (Salticidae) are renowned for their elaborate visual displays (Jackson & Pollard 1997), having complex eyes (Homann 1928; Land 1969a,b, 1985; Blest 1985) and unique vision (Crane 1949; Drees 1952; Jackson & Blest 1982; Forster 1985), It may not be surprising that vision has an important role in these spiders' intraspecific interactions (Forster 1982b; Jackson 1982a), but evolution of visual communication has not precluded use of pheromones and other infochemicals by salticids (Jackson and Pollard 1997).

There is evidence that silk-bound pheromones of salticids elicit male courtship and enable males to discriminate between nests of conspecific and non-conspecific females, conspecific females and males, and subadults close to moulting and not close to moulting (Jackson 1987). Olfactory pheromones have received less attention. Crane (1949), however, working with *Corythalia xanthopa*, found evidence that males are affected by olfactory primer pheromones from females. Primer pheromones are chemical stimuli that lower a male's threshold of response to visual releasers of courtship, releasers being defined as the stimuli that actually elicit the displays (see Wilson 1971). In Crane's study, males' readily courted recently deceased females, without first touching their cuticles, then attempted to mate with them. Aged corpses, however, failed to elicit courtship. Presumably, volatile chemical cues provided by recently deceased females were no longer present in aged corpses.

More recently, olfactory pheromones have been shown experimentally to influence the foraging behaviour of four species of *Portia* when in other species' webs. When olfactory cues from a conspecific female are present, other females become less inclined to begin making aggressive-mimicry signals and instead attempt to capture prey (Willey and Jackson 1993). However, there have been no detailed experimental studies on how olfactory pheromones might influence display and direct conflict between conspecifics is unknown for *Portia* and other salticids.

There is, however, observational evidence that in *Asemonea tenuipes* (Jackson & Macnab 1991), a Sri Lankan salticid, olfactory pheromones release the males courtship and enable males to locate females, but there have been no experimental studies that confirm this for *A. tenuipes* or any other salticid species.

That there is evidence of reliance on olfactory pheromones in *Asemonea tenuipes* and in *Portia* is interesting because these species belong to salticid subfamilies (*Asemonea* is a lyssomanine and *Portia* is a spartaeine) that have especially many putatively primitive characters (i.e., for salticids, these can be called 'primitive families').

Almost 5,000 salticid species have been described (Coddington and Levi 1991; Zabka 1993), making this the largest spider family. Behaviourally these spiders are highly diverse, but it appears to be particularly in putatively primitive groups that unusual behaviour has been found, including web-building, specialised predatory forays into other spiders' webs, and the use of vibratory aggressive mimicry to deceive victim spiders in alien webs (Jackson and Pollard 1996). As a working hypothesis, it might be proposed that the salticid species that are especially reliant on olfactory pheromones as releasers and primers of display are in more primitive salticid groups (see Pollard et al. 1987).

Identifying salticid species that rely strongly on olfactory pheromones might be highly advantageous in relation to my thesis objectives. The difficulty in assuring that a salticid in an experiment actually perceives a lure was discussed earlier (Chapter 2-4). Olfactory cues may present lesser difficulty.

Sight, being a highly directional sense (Mueller et al 1967; Sinclair 1985), requires that an animal must be looking in exactly the right direction and attentive to the image on its retina before it can detect the presence of a

relevant small stimulus such as a conspecific female. This is especially true for salticids because the area of the eye that processes detailed images (the fovea) covers only about 2 degrees of arc (Land 1969a; Land 1969b). It is difficult to ascertain that an image has indeed been cast on the salticid fovea because, although the corneal lenses are fixed parts of the salticid's cuticle, the eye tubes are highly mobile.

Odours are volatile plumes subject to rapid dissipation and diffusion by wind (Wilson & Bossert 1963; Alberts 1992; Svensson 1996). Therefore, olfactory cues may be especially useful at revealing from a distance the presence and identity of unseen conspecifics.

This has potentially important implications for the effectiveness of experimental design. For species that rely on olfactory cues, experiments comparable to those in Chapters 2-4 might be run much more efficiently but with the priming stimulus being pheromones instead of lures.

Here findings are presented from an experiment where *Euophrys parvula*, *Jacksonoides queenslandicus* and *Portia fimbriata* were used, the same three salticid species used in earlier chapters. The experiment here parallels experiments in the earlier chapters except that now the cues from potential mates are potential olfactory pheromones instead of lures made from dead, conspecific females.

Pairs of male spiders were tested in the presence and then again in the absence of olfactory cues from a conspecific female. Intrasexual conflict behaviour is studied and any measured increase in aggression in the presence of the female's olfactory cues was interpreted as escalation of conflict functioning to assist the male obtain access to the female (i.e., the hypothesis is that the female is a resource for which the males are fighting).

MATERIALS AND METHODS

General

All spiders tested were adults from laboratory cultures established by collecting from field. *E. parvula* cultures were established from specimens collected at a site on the West Coast, South Island, New Zealand (Chapter 2). *P. fimbriata* and *J. queenslandicus* cultures were established from specimens collected at a site in Queensland, Australia (Jackson 1988). Standard rearing and maintenance procedures were used in the laboratory under controlled light, humidity, and temperature (lights came on at 0800h and went off at 2000h). For more details, see Jackson & Hallas (1986).

Most of the details of these paired conflict tests are given elsewhere (Wells 1988; Chapter 2-4). For this reason, only essential details and modifications of the design are given here.

Study animals

1) *Euophrys parvula.*

The displays that males of *E. parvula* adopt during intrasexual encounter have been described in detail elsewhere (Wells 1988; Jackson and Wiley 1995). A list of the ranked behaviours used by Wells (1988), along with a brief description, follows:

1. Postured with legs hunched (rank 1). The first three pairs of legs were brought forward, flexed and held close to the body. Adoption of this posture, which will be called the 'hunch display', was usually performed while the two males are distant from each other. This was typically the display first adopted when a male encountered another conspecific male. However, hunch display is not exclusive early after encounter, but instead, tended to be the dominant display throughout the interaction whenever spiders were at least 10 mm apart.
2. Postured with legs erect while no more than 10 mm from the other male (rank 2). The third pair

of legs were held out stiffly above the substrate at about 30° to the horizontal. Often, this display was also used briefly at a distance greater than 10 mm in conjunction with the hunch posture, but at this greater distance it did not qualify as rank 2. While the two spiders were 10 mm or less from each other, this posture (called 'erect display') tended to be maintained for prolonged periods, during which time the two spiders usually manoeuvred around each other actively.

3. Stave (rank 2). When this occurred the spiders were 5-10 mm apart with legs III erect. To stave, a spider suddenly raised and lowered the erect leg closest to the other male. At the same time the staving spider moved rapidly to one side of the other male, raising the closer side of the body simultaneously while stepping so that when this leg next moved suddenly down it came down against the erect leg of the other male. Staving was often interspersed within bouts during which males manoeuvred around each other, successive lowering of the erect legs coming at intervals of 1-20 s.
4. Embrace (rank 3). The spiders brought the front of their cephalothoraces together and pushed against each other. Legs III often remain erected. Sometimes each spider's erect leg III contacted the other spider's erect leg III. Occasionally, legs I were also erect and touching.
5. Cheliceral-lock display (rank 4). Each spider interlocked its chelicerae with the other male's chelicerae and each spider appeared to attempt to lift the other up. The bodies of the two spiders usually ended up in a tent-like configuration. Occasionally one spider lifted the other off the ground.
6. Fight (rank 5). While the spiders performed the cheliceral-lock display, one male occasionally succeeded in pushing the other male over onto his dorsal surface. Usually the up-ended spider righted itself and ran away. A fight occurred if the rival walked over the up-ended spider, at which point the pair would grapple wildly, venter-to-venter, for several seconds until one male ran away. Fights normally resulted in leg injuries to one or both males, evidenced by immobility of a leg when trying to move after the fight.

2) *Portia fimbriata.*

P. fimbriata is an important salticid to study because this species is known to use information from airborne and chemotactile pheromones during courtship and mating (Pollard et al 1987; Clark & Jackson 1995a; Jackson & Pollard 1997) as well as during predatory sequences (Clark et al in press; Jackson et al in prep).

A list of the displays seen in male-male conflicts, along with the ranking of each display, follows:

1. Posturing with legs hunched (rank 1). The first three pairs of legs were brought forward, flexed and held close to the body. Adoption of this posture, which was called the 'hunch display', was usually performed while the two males were distant from each other, and was typically the display first adopted when a male encountered another conspecific male. However, hunch display was not exclusive to early in encounters, but instead tended to be the dominant display throughout the interaction whenever spiders were at least 10 mm apart.
2. Posturing with legs erect (rank 1) while no more than 10 mm from the other male (rank 2). The first pair of legs alone, or more often the first two pairs of legs together, were held out stiffly above the substrate at about 45° to the horizontal and were angled between 45-90° out to the side of the males' body. This display was often used briefly at a distance greater than 10 mm in

conjunction with the hunch posture, but at this distance it did not qualify as rank 2. While 10 mm or less, from each other, this posture (called 'erect display') tended to be maintained for prolonged periods, during which time the two spiders usually manoeuvred around each other actively.

3. Embrace (rank 3). The spiders brought the front of their cephalothoraces together and pushed against each other. As the spiders approached the erect legs of the two spiders displaying overlapped as they got closer. The cephalothoraces of the two spiders were often raised, with the abdomen tilted down. These displays only lasted 5-10 s.
4. Grapple (rank 4). Embracing spiders grappled by moving their overlapping forelegs forward over the opponents' forelegs and forcefully flexing these legs. This display sometimes pulled off one of the opponent's legs.
5. Fight (rank 5). While embracing one male occasionally pushed the other male over onto its dorsal surface. Usually, the up-ended spider righted itself and ran away. However, a fight occurred if the rival spider walked over the up-ended spider. The pair fought by grappling wildly until one male ran away several seconds later. While fighting, the spiders were venter-to-venter.

3) *Jacksonoides queenslandicus.*

A list of the displays seen in male-male conflicts along with the ranking of each display follows:

1. Posturing with legs hunched (rank 1). The first three pairs of legs were held highly flexed and to the side of the body (perpendicular to the sagittal plane of the body). Adoption of this posture (hunch display), was usually while the two males were distant from each other and was typically the display first adopted when a male encountered another conspecific male. However, hunch display was not exclusive to early after encounter, but instead tended to be the dominant display throughout the interaction at any time when the spiders were at least 10 mm apart.
2. Posturing with legs erect (rank 1) while no more than 10 mm from the other male (rank 2). The first pair of legs alone, or sometimes first two pairs of legs, were held out stiffly above the substrate (10-45° to the horizontal) and were angled approximately 45° directly from forward. (This display was often used briefly at a distance greater than 10 mm in conjunction with the hunch posture, but at this distance did not qualify as rank 2.) While 10 mm or less, from each other, this posture (called 'erect display') tended to be maintained for prolonged periods, during which time the two spiders usually manoeuvred around each other actively.
3. Embrace (rank 3). The spiders brought the front of their cephalothoraces together and pushed against each other. The first pair of legs were held erect out from the side of the body and usually remained in contact with the opponents' legs I during this display. Embraces were often performed briefly (1-2 s in duration) with bouts of short-duration, repeated embracing sometimes occurring.
4. Wrestle (rank 4). Wrestling occurred while the spiders embraced. The two spiders locked their chelicerae (with fangs not exposed) and twisted their cephalothoraces alternately clockwise then anticlockwise (about 20° in each direction).
5. Fight (rank 5). Fights between the two male *J. queenslandicus* followed a similar pattern to that found in fights between male *P. fimbriata.* Fights usually occurred directly after

wrestling and involved the two spiders grappling venter-to-venter. Like fights between *P. fimbriata* males, one *J. queenslandicus* male would normally decamp rapidly thus ending the fight.

Basic experimental procedure

Encounters between two males were staged in a test arena, a Perspex cage (215 mm long X 110 mm wide X 30 mm high) with a removable glass top and removable Perspex end pieces. The bottom of the arena was opaque and an opaque cardboard divider (25 mm high) bisected the centre of the cage and extended out of a slit in the front face of the arena to the outside. When the divider was in place, the two test spiders could see the top of the cork but not each other.

The basic set up was modified by shortening the arena to 144 mm long X 110 mm wide X 20 mm high and the addition of a stimulus chamber (Fig. 26). Shortening the chamber had the effect of decreasing the time that the test spiders took to find each other. The stimulus chamber consisted of a darkened glass vial (40 mm high and 25mm in diameter). The stimulus was stoppered using a removable, lightweight nylon mesh, held in place using a small rubber band. A hole (10 mm diameter) was drilled in the bottom of the vial and lightweight nylon mesh was glued over the hole. The stimulus chamber was set up in such a way as to allow air to flow freely through the vial and into the test arena. A plastic elbow connected the stimulus chamber to the arena. This elbow was round in cross section and fits the stimulus chamber snugly (25 mm inner diameter/35 mm outer diameter). The elbow was approximately 60 mm high and 60 mm wide when viewed side on. A hole (25 mm) was in the back wall and a plastic tube (25 mm in diameter) was placed in this hole. The tube had fine brass mesh glued over one face and when in place the mesh was flush with the back wall. The tube projected from the back wall of the arena and the end of the plastic elbow that was not connected to the stimulus chamber fits over the tube, connecting the stimulus chamber to the arena.

Recording, analysis and terminology

Interactions were staged by allowing pairs of individuals of the same sex and species (the "test spiders") to encounter each other in the test arena. Natural variation in size and coloration made the identity of the two individuals in any interaction identifiable.

All experiments followed a paired-comparison design: on one day, the two spiders were tested in the presence of a cue from a potential resource (olfactory cue from the stimulus spider); on the succeeding or preceding day (decided at random), the same pair was tested in the absence of this cue. All tests were conducted between 0900h and 1500h. The spiders were tested only once within a single 24-h period. No spiders were tested more than twice. When an individual spider was tested more than once, it was always paired with a different conspecific.

Details about interactions were verbally recorded on tape (Dictaphone) and later transcribed. Key pieces of information used in data analysis were the number of times the spiders embraced, the distance at which the spiders first displayed to one another and the closest distance the spiders were to each other during the test. For a list of displays likely to occur in an interaction, along with brief descriptions for these displays, see above. The distance between the two spiders refers to the distance from the front of the cephalothorax of one spider to the front of the cephalothorax of the second spider.

Appropriate statistics for pair-wise data were used (McNemar tests for significance of changes & Wilcoxon tests for paired comparisons: Sokal & Rohlf 1995). The P-values given are after Bonferroni adjustments whenever the same data are used for multiple comparisons (Rice 1993).

Methods

This set of experiments examined the effect that odours from conspecific females have on intrasexual contests between pairs of male jumping spiders. The methods for this are derived from those of Willey and Jackson (1993).

Spiders were manoeuvred into place using a fine, camel hair paintbrush. Great care was taken when moving these animals from their cages into the test arena and the stimulus chamber (and vice versa) so as to minimize disturbance.

A conspecific female (stimulus spider) was placed within the stimulus chamber. The odour from the stimulus spider was allowed to diffuse throughout the arena for a period of 1 h. This provided the olfactory cue. During control tests, there was no stimulus spider in the stimulus chamber, but the chamber was allowed to sit at least 1 h before testing began.

The two test spiders were placed on opposite sides of this divider and allowed to acclimatise to their surroundings for 10 min. After this 10 min period had elapsed, the divider was removed, allowing the spiders to see one another. The test started when the spiders first displayed to one another. Details concerning the interactions between the test spiders were recorded.

RESULTS

Euophrys parvula

Contests did not differ in the level of escalation (Fig. 27) (Wilcoxon's signed ranks test, 1 tailed, P=0.29, N=20) and there was no difference between tests in the number of embraces that occurred (Fig. 28) (Wilcoxon's signed ranks test, 1 tailed, P=0.22, N=20). In addition, the distance from which the spiders first displayed (Fig. 29) (Wilcoxon's signed ranks test, 1 tailed, P=0.81, N=20) and the distance to which the spiders closed during contests (Fig. 30) (Wilcoxon's signed ranks test, 1 tailed, P=0.64, N=20), did not differ significantly between tests.

Portia fimbriata

P. fimbriata males reached greater levels of escalation (Fig. 31) (Wilcoxon's signed ranks test, 1 tailed, P=0.004, N=18) in the presence than in the absence of the odour of a conspecific female. The number of embraces (Fig. 32) (Wilcoxon's signed ranks test, 1 tailed, P=0.004, N=18) and the distance to which the spiders closed during contests (Fig. 33) (Wilcoxon's signed ranks test, 1 tailed, P=0.006, N=18) also differed significantly between tests. However, the distance at which the spiders first displayed did not differ significantly between the control and the experimental tests (Fig. 34) (Wilcoxon's signed ranks test, 1 tailed, P=0.74, N=18).

Jacksonoides queenslandicus

J. queenslandicus males showed no increase levels of escalation (Fig. 35) (Wilcoxon's signed ranks test, 1 tailed, P=0.03, N=19) in the presence of the odour of a conspecific female. Nor was there a significant difference in the number of embraces (Fig. 36) (Wilcoxon's signed ranks test, 1 tailed, P=0.01, N=19) or the distance at which the spiders first displayed in each contest (Fig. 37) (Wilcoxon's signed ranks test, 1 tailed, P=0.01, N=19). There was also no significant difference in the distance to which the spiders closed between the control and the experimental tests (Fig. 38) (Wilcoxon's signed ranks test, 1 tailed, P=0.06, N=19).

DISCUSSION

Results of these experiments show that the presence of olfactory cues from a conspecific female has a significant influence on male-male conflict in two out of three of the species of salticid tested. One possible interpretation of

these findings is that they are evidence that intrasexual selection has driven the evolution of male-male conflict behaviour in jumping spiders. It would appear that males are directly competing with one another for mating opportunities as was predicted by sexual selection theory (Gould & Gould 1989; Andersson 1994). However, some of the same problems that have plagued these previous studies apply here as well.

This study has controlled for the possibility that the act of courting (or other displays) may somehow prime males to increase the intensity of male-male conflict on seeing another male (Chapter 3) because the test spiders were not courting in both the control and experimental test of this study. Detection and attention to the olfactory cue might be more confidently assumed than had been the case for optical cues. However, other problems remain. The first could be considered to parallel the general-agitation problem. The laboratory where the experiments were conducted was full of many species of spiders. We cannot guarantee that the spiders are not simply reacting to the odour of some other spider. Although, the paired test design coupled with the fact that the odour from the stimulus spider would be the strongest odour in the arena makes this hypothesis improbable, the only way to completely rule out this problem would be to test the spiders in sterile air. This would be hard to achieve.

The second problem is similar to one found in tests using lures. We do not know how specific the findings of this study are. As with the optical-cues study, one cannot rule out the possibility that olfactory cues from any conspecific, or any spider for that matter, causes the escalation in male-male conflict. Further testing is needed with different olfactory cues. It would also be useful to examine the effect of olfactory cues on female-female conflict.

We can say from this study that some male salticids have yet another tactic in a conditional strategy employed during intrasexual conflict. This tactic appears to be similar to that which applied in the optical-cue tests (Wells 1988; Chapters 2, 3, 4). On receiving information about the presence of a conspecific female (and possibly other spiders), males have a rule to escalate the level they will go to in intrasexual conflict.

Interestingly, of the three species studied, *E. parvula* did not appear to detect the presence of a female using olfactory cues. Crane (1949) suggested that reliance on olfactory cues in courtship is a 'primitive' trait and as such more likely to occur in 'primitive' salticids. Work by Jackson and Macnab (1991) also suggest greater reliance on olfactory cues may be the primitive condition. Alternatively, this may be an ecological trend and unrelated to systematics (see Jackson 1982a).

In other animal groups besides salticids, it appears that males use olfactory cues to determine the presence of a female. For example, Taylor (1980) found that male rats used olfactory cues to determine the reproductive potential of conspecific females (males differentiated between oestrus and dioestrous females). Male-male aggression in rats increased when a female in oestrus (or soiled bedding from an oestrus female) was placed in a cage with pairs of males compared with a dioestrous female (or soiled bedding from the dioestrous female). Similar results have been reported in the spider mite, *Tetranychus urticae* (Potter 1981). Male spider mites guard sub-adult females that are undergoing their moult into an adult. Apparently these spider mite males can determine how close a female is to sexual maturity using chemosensory cues and the males fight harder when in the presence of a female that has nearly completed moulting than when in the presence of a female that is midway through the moulting process. That is, these mites appear to have the ability to assess the quality of the resource they are fighting for (i.e. the female) rather than simply whether a female is present or absent.

An interesting experiment would be to determine whether salticid males 'judge' the relative value of females as in the spider mite, where a virgin female is presumably more valuable than a female that has mated previously. This might be likely, as it is known that jumping spiders can gather highly detailed information from olfactory and chemotactile cues. Salticids can discriminate their own draglines from conspecifics (Clark & Jackson 1994a), and females can distinguish their own eggs from a conspecific female's (Clark & Jackson 1994b). Jumping

spiders can recognise the sex of a conspecific from draglines (Clark & Jackson 1995a), and discriminate between familiar and unfamiliar conspecifics (Clark & Jackson 1995b. They can even determine the fighting ability of potential opponents from dragline before meeting them (Clark & Jackson 1999). *P. fimbriata* is able to detect the presence of a common prey, *J. queenslandicus*, using olfactory cues alone (Clark et al. 1999). Some salticids clearly rely heavily on information gathered from chemical cues.

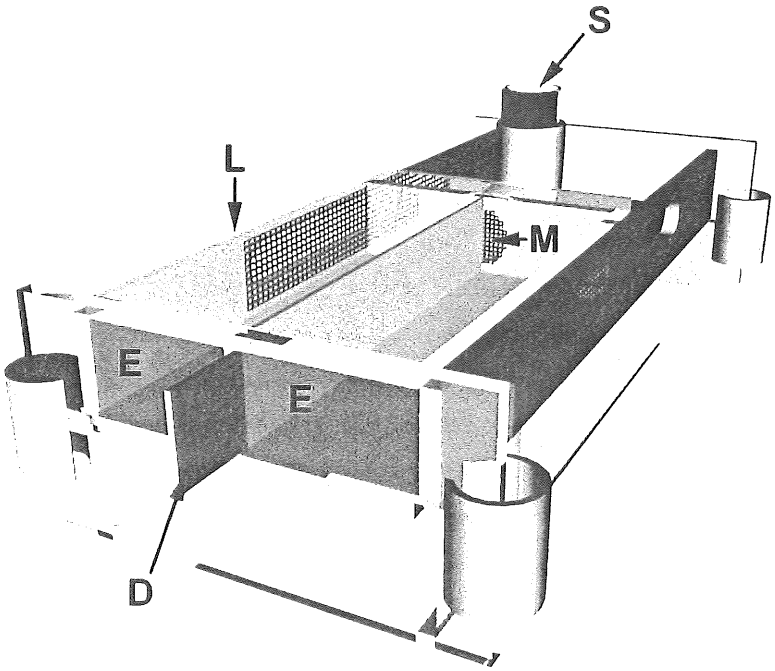

Fig. 26: Drawing of transparent Perspex "modular cage". D: Opaque cardboard divider bisected the arena, which allowed spiders to be placed one on either side of the area and allowed both animals to see the cork (and lure, if present) without seeing each other. E: Clear Perspex end pieces that were removed to allow the spiders into one half of the arena and replaced to keep spiders in the arena. These end pieces were held in place by plastic clamps. L: Transparent glass lid that formed the roof of the arena that allowed observation but prevented the animals from escaping. M: Copper mesh that allowed olfactory cues to enter the arena from the stimulus chamber. S: Stimulus chamber, a darkened glass vial containing the stimulus spider that supplied the olfactory cue for the test spider to react to. During the control test the chamber was left empty.

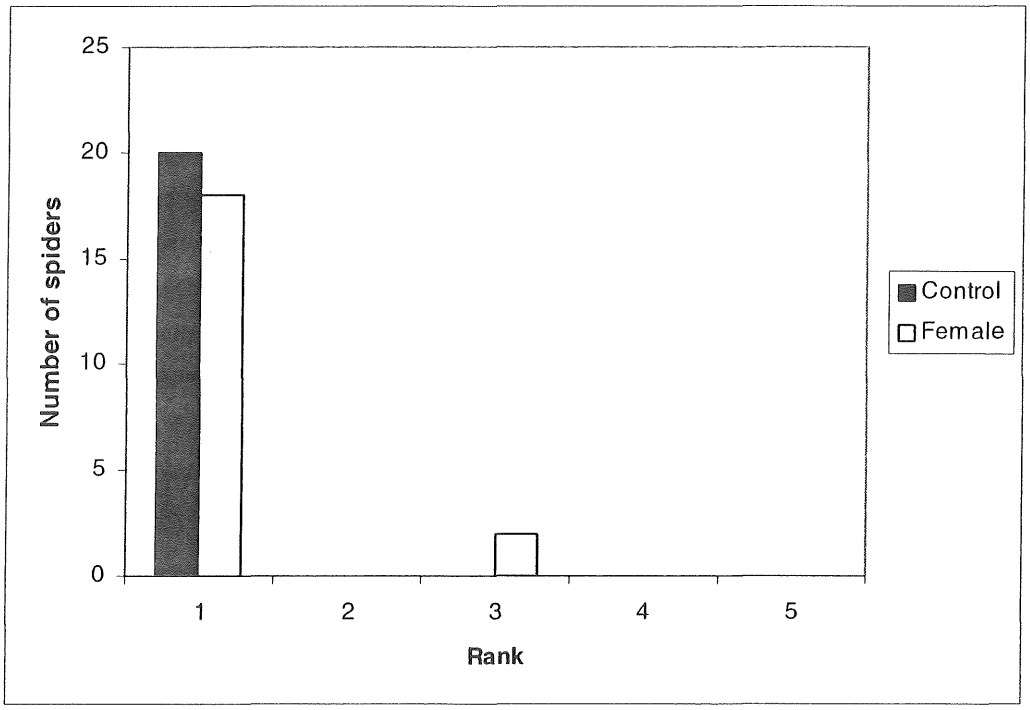

Fig. 27: Number of contests (N=20) of *Euophrys parvula* males at each level of escalation with female odour present and absent.

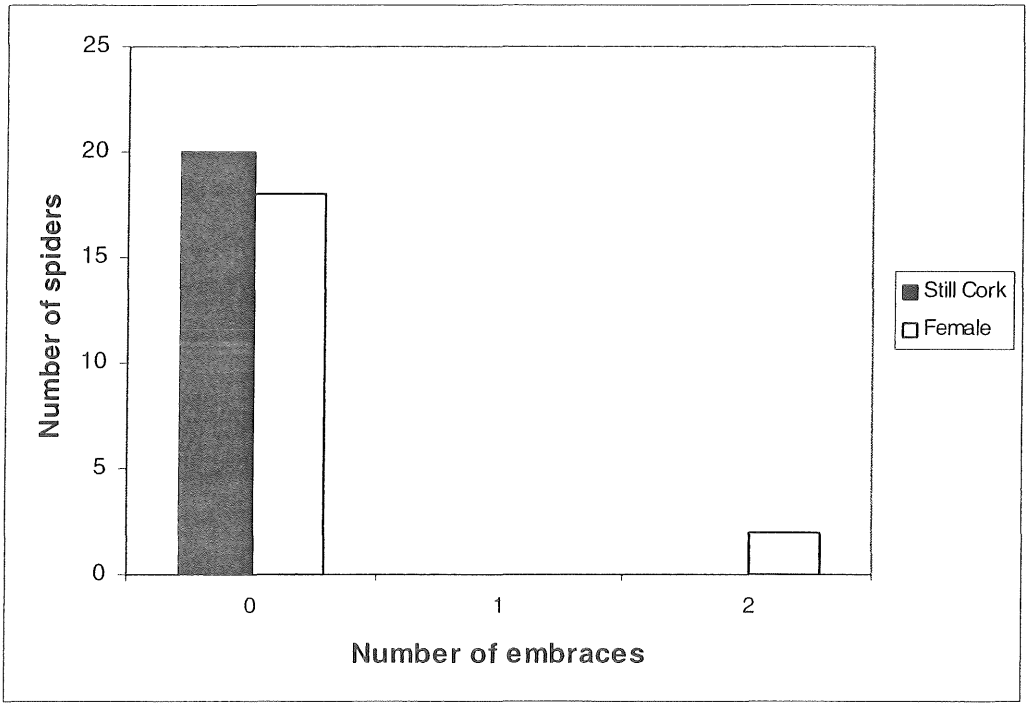

Fig. 28: Number of embraces in each contest (N=20) of *Euophrys parvula* males with female odour present and absent during contests.

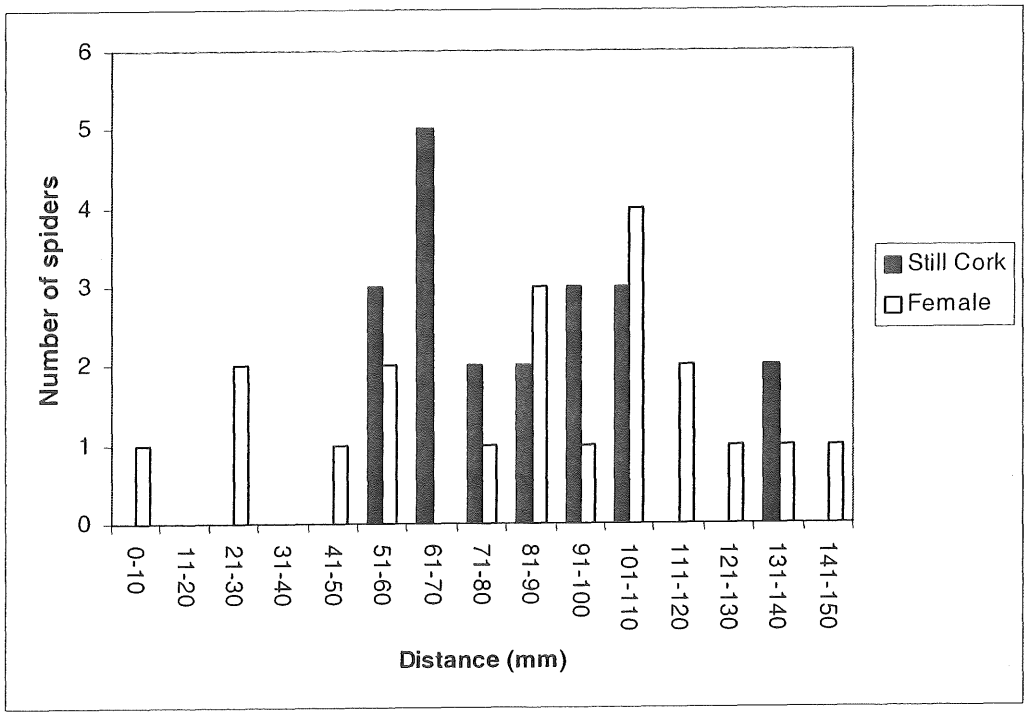

Fig. 29: Comparison of the distance to which pairs of *Euophrys parvula* males first displayed with female odour present and absent (N=20).

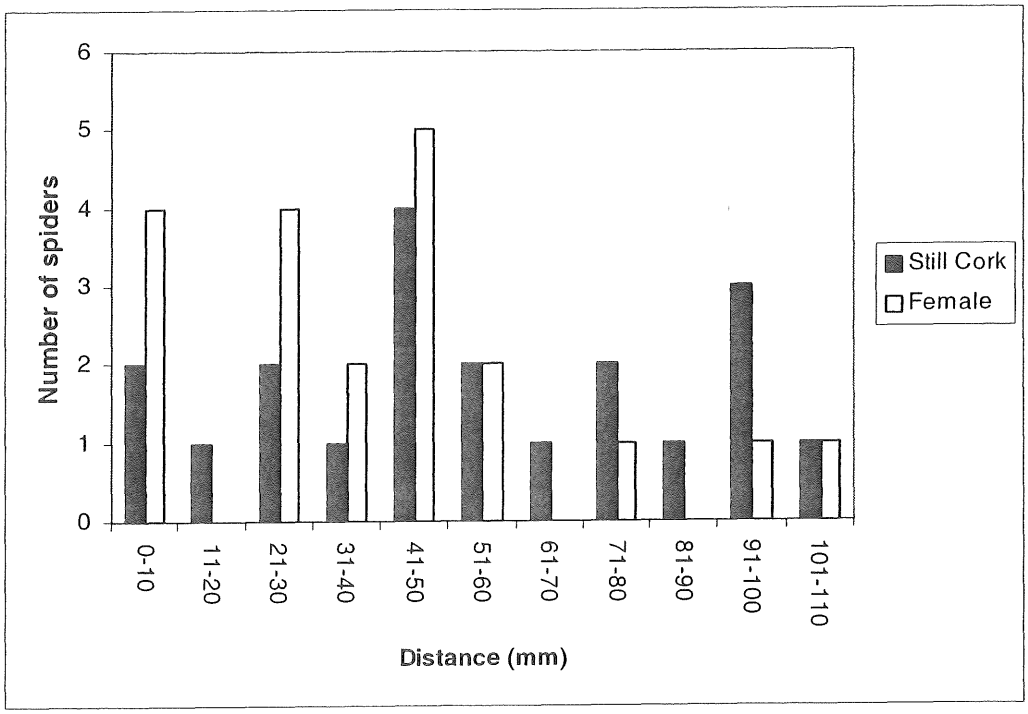

Fig. 30: Comparison of the distance to which pairs of *Euophrys parvula* males closed in tests with female odour present and absent (N=20).

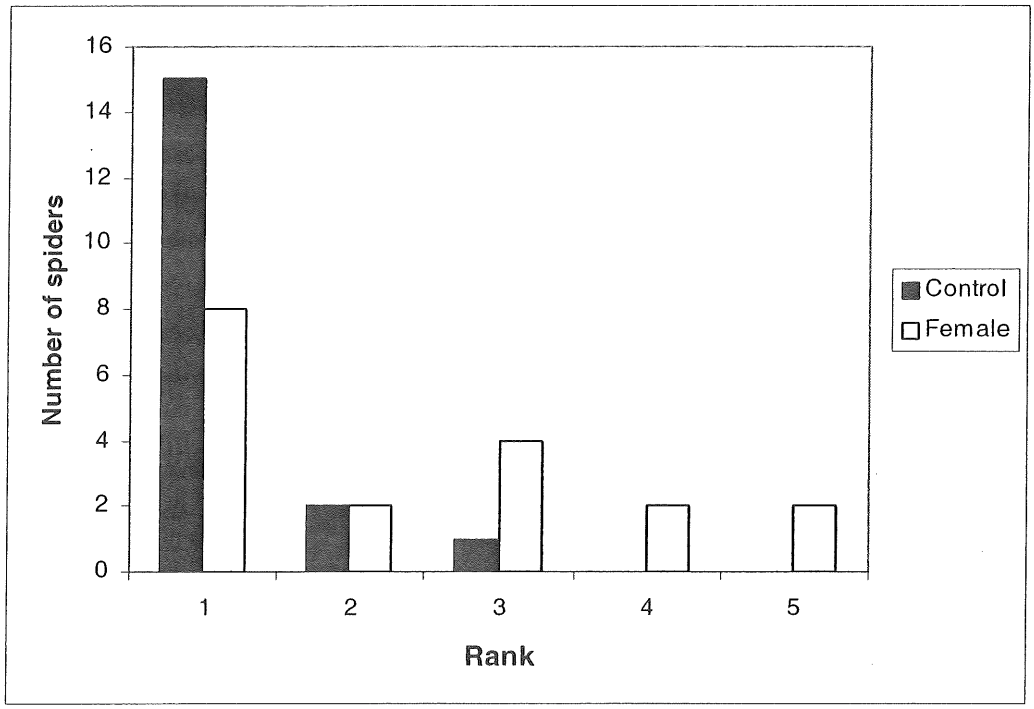

Fig. 31: Number of contests (N=18) of *Portia fimbriata* males at each level of escalation with female odour present and absent.

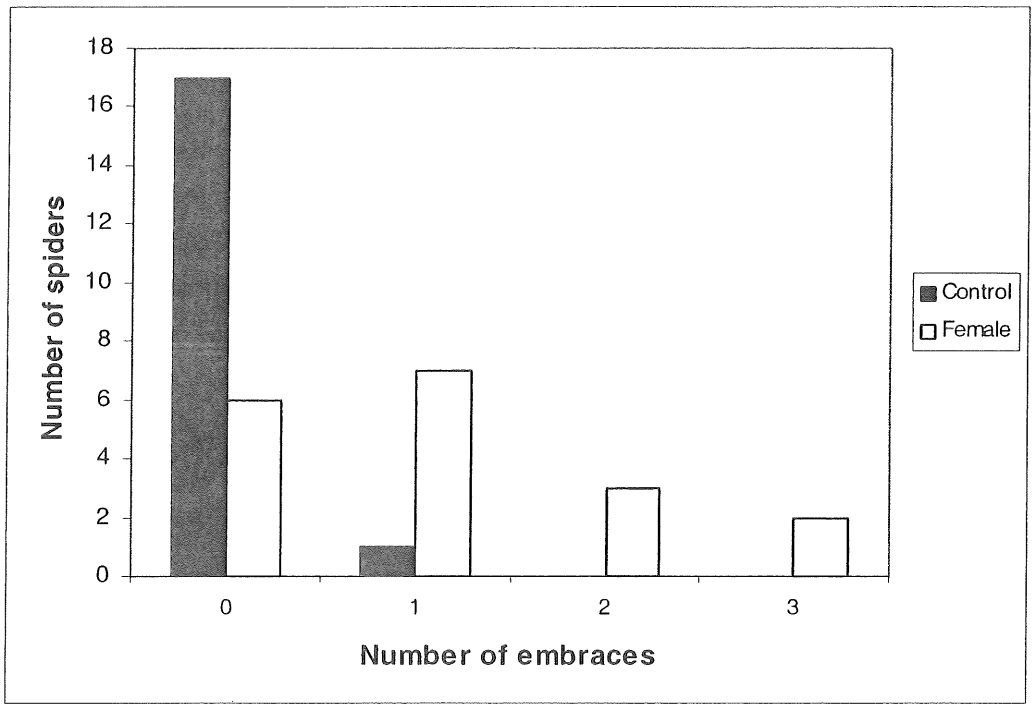

Fig. 32: Number of embraces in each contest (N=18) of *Portia fimbriata* males with female odour present and absent.

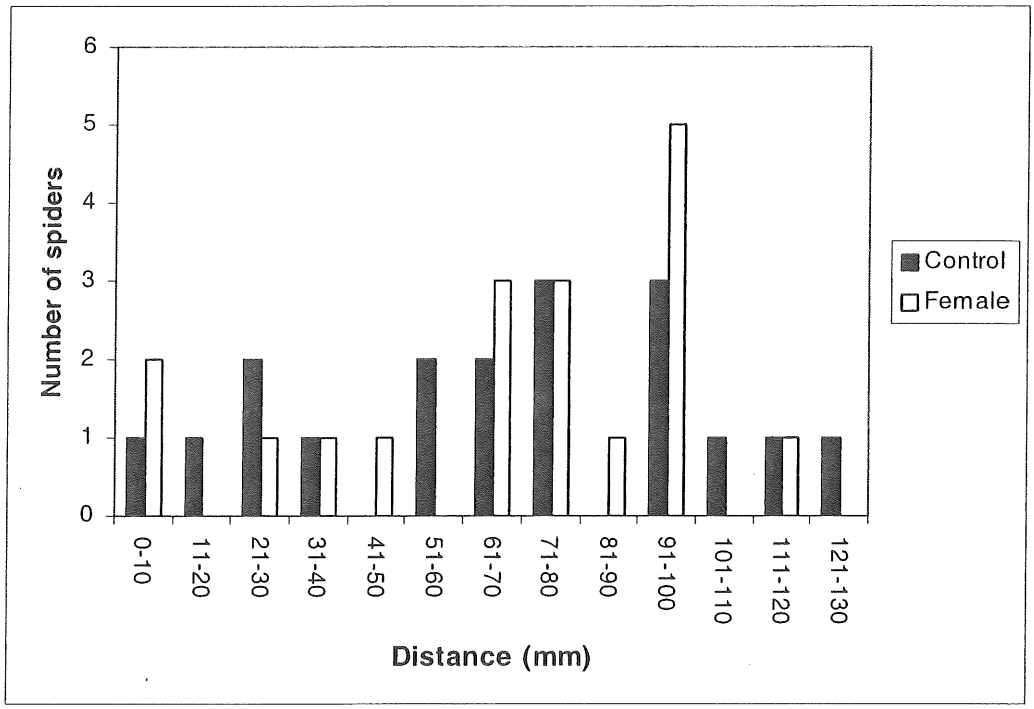

Fig. 33: Comparison of the distance to which pairs of *Portia fimbriata* males first displayed with female odour present and absent (N=18).

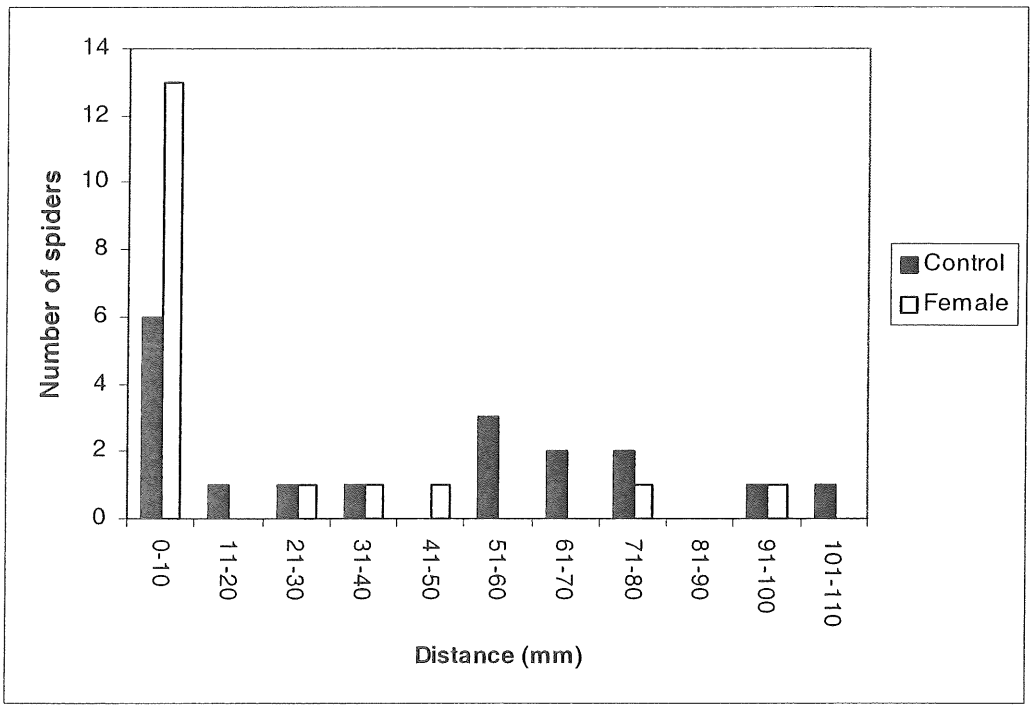

Fig. 34: Comparison of the distance to which pairs of *Portia fimbriata* males closed in tests with female odour present and absent (N=18).

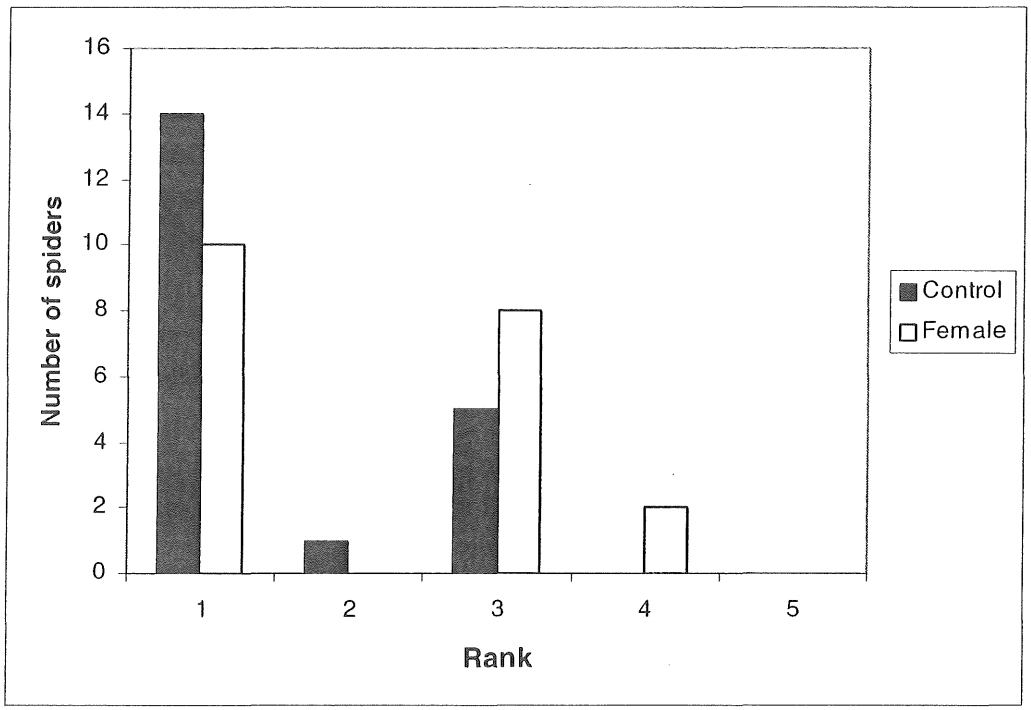

Fig. 35: Number of contests (N=20) of *Jacksonoides queenslandicus* males at each level of escalation with female odour present and absent during contests.

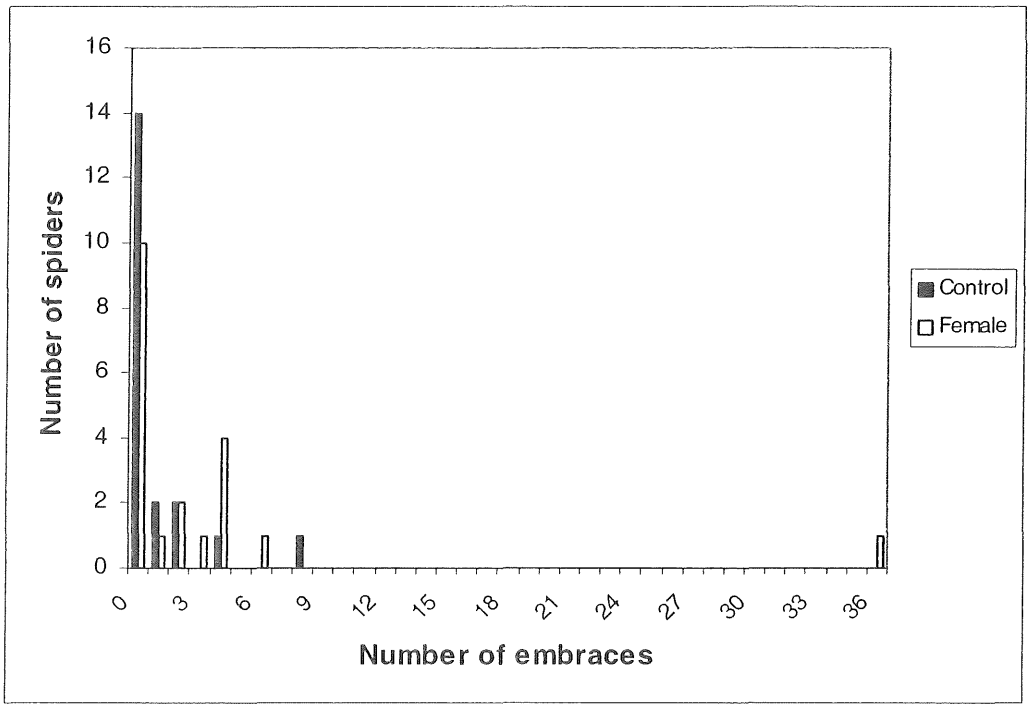

Fig. 36: Number of embraces in each contest (N=20) of *Jacksonoides queenslandicus* males with female odour present and absent.

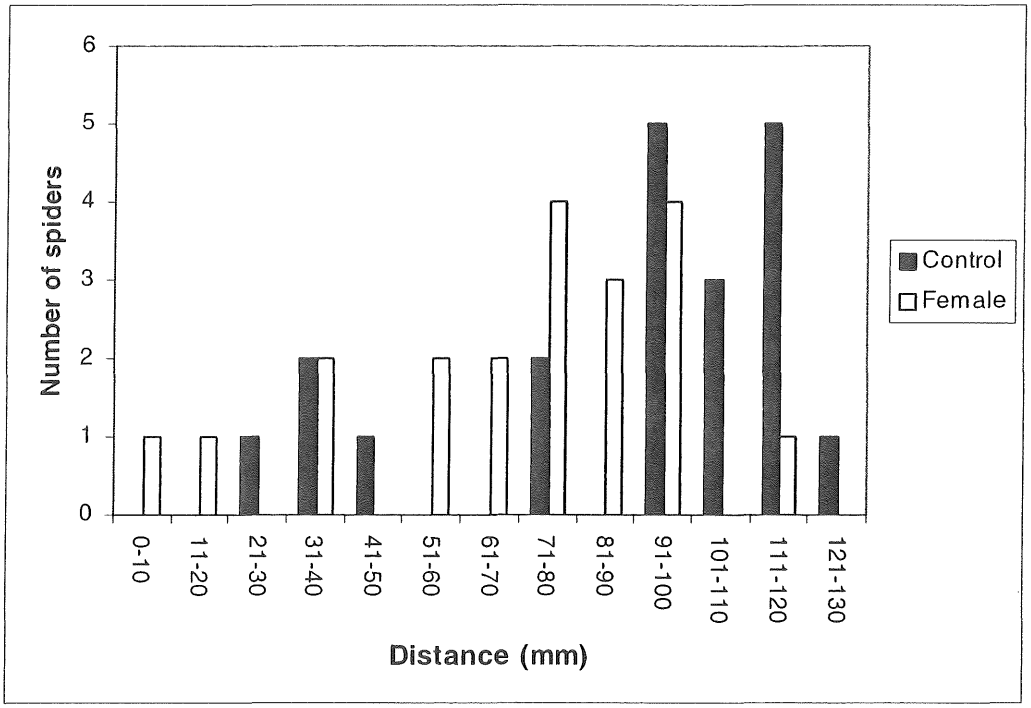

Fig. 37: Comparison of the distance to which pairs of *Jacksonoides queenslandicus* males first displayed with female odour present and absent (N=20).

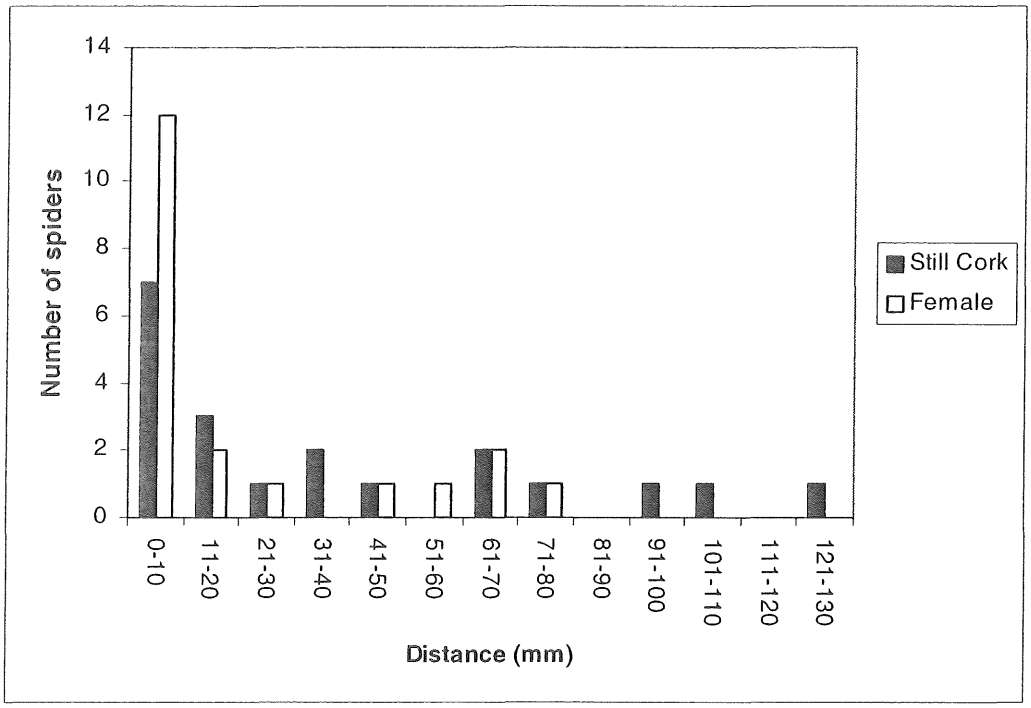

Fig. 38: Comparison of the distance to which pairs of *Jacksonoides queenslandicus* males closed in tests with female odour present and absent (N=20).

Chapter 6: Influence of olfactory cues from prey on intrasexual conflict in *Portia fimbriata,* a salticid from Queensland, Australia.

INTRODUCTION

Conditional strategies are interesting because they have the potential to reveal specific selection pressures that have shaped the evolution of particular features of an animal's behaviour (see Alcock 1998). Studying the rules governing conditional strategies can be envisaged as asking an animal, in experiments, what resources matter to it. In a species with a conditional strategy each individual has a set of distinct tactics and a set of decision rules specifying the circumstances under which to use each tactic in the set (Dominey 1984): different tactics appear to be adaptively fine-tuned to the specified conditions. The behaviour of salticids is an especially pronounced example of conditional strategies.

The Salticidae, with nearly 5,000 described species (Coddington & Levi 1991; Zabka 1993), is the largest family of spiders. In general, spider eyes lack the structural complexity required for acute vision, but salticids possess unique, complex eyes with resolution capabilities with no known parallels in other animals of comparable size (Land 1969a,b; Blest et al. 1990; Jackson & Harland 1998; Harland et al. 1999). Much of the intricate predatory behaviour of salticids is guided by vision (Forster 1982a; Richman & Jackson 1992; Jackson and Pollard 1996).

The most complex conditional strategy known for a salticid, and also the most acute eyesight, is found in the Queensland population of *Portia fimbriata* (Jackson & Wilcox 1998). Although, most salticids are cursorial predators of insects (Richman & Jackson 1992), those in the genus *Portia* build prey-capture webs, in addition to cursorial hunting and also practise araneophagy by invading other spider's webs and making aggressive-mimicry signals (Jackson & Hallas 1986). By manipulating the web using legs and palps, *Portia*'s aggressive-mimicry signals manoeuvre the resident spider into position before *Portia* strikes (Jackson & Wilcox 1998). The particular way *Portia* uses aggressive mimicry is further adjusted to the particular species of spider resident in the invaded web, the size of the resident spider relative to *Portia,* and how the resident spider responds to initial manipulation of the web (Jackson & Wilcox 1994; Jackson & Wilcox 1998).

P. fimbriata from Queensland is unique because it also hunts other salticids in addition to hunting web-building spiders. Unlike web building spiders, salticids are prey that can see as well as *Portia*, but the Queensland *P. fimbriata* has a special tactic; called 'cryptic stalking', which enhances *Portia*'s resemblance to detritus and facilitates capture of this special type of prey (Jackson and Blest 1982). 'Cryptic stalking' is not used when non-salticid spiders or insects are stalked.

The Queensland *P. fimbriata*'s conditional predatory strategy is fine-tuned to aid capture of two common Queensland salticids, *Euryattus* sp. and *Jacksonoides queenslandicus*. *Euryattus* sp. females build nests made from dead, rolled-up leaves that are suspended by a few heavy silk lines. On seeing one of these nests, the Queensland *Portia* manoeuvres above the nest and, using a dragline, drops down on top of it. Once on the nest, *Portia* mimics the courtship behaviour of a *Euryattus* male. This lures the female out so that *Portia* can attack it (Jackson & Wilcox 1990; Jackson & Pollard 1996).

The Queensland *Portia* seems also to have evolved predatory tactics specifically for use when preying on *J. queenslandicus*. Contact chemical and olfactory cues from *J. queenslandicus* cause *Portia* to linger in areas where these cues are present. Contact cues from *J. queenslandicus* draglines cause *Portia* to retract its palps, which is part of the cryptic stalking posture adopted when hunting salticids. Olfactory cues also enhance *Portia*'s attention to visual cues from *J. queenslandicus* (Jackson et al. in prep.).

Another response triggered by the draglines of *J. queenslandicus* is undirected leaps (erratically leaping with no apparent target). When *J. queenslandicus* detects movement in the environment, it typically responds by turning to face the source and waving its palps (Clark et al. in press). By making undirected leaps, *Portia* elicits these responses from *J. queenslandicus* and this response makes *J. queenslandicus* more detectable to *P. fimbriata.* Draglines and odour from other salticid species do not elicit these responses from the Queensland *Portia.* Evidently, *J. queenslandicus* is an important resource to the Queensland *P. fimbriata.*

An especially important prediction from game theory can be summarised as follows: the cost a contestant is willing to incur by fighting (contest cost) will increase when resource value increases. In Chapters 2-5 hypotheses about potential mates being resources for which salticids compete were considered. The present chapter extends the earlier work by exploring the possibility that food may also be an important resource that influences salticid interactions. More specifically, the question of whether olfactory cues from *J. queenslandicus* influences intraspecific interactions of Queensland *P. fimbriata* is considered.

Adult jumping spiders show a marked difference between the sexes in the relative importance of food resources. Upon reaching maturity, male salticids seem to become less interested in food and more interested in searching for mates (Elgar 1998); females seem to be more interested than males in food. This trend appears to apply strongly to *Portia* (Jackson and Hallas 1986). These arguments suggests that cues from *J. queenslandicus* will strongly influence female-female behaviour on the Queensland *P. fimbriata* but not so strongly influence male-male behaviour in the Queensland *P. fimbriata.* This prediction is tested in experiments in experiments where the potential cues are olfactory. Additionally this study will attempt to gain a tighter control of the variables by testing the reaction of the salticid to its reflection in a mirror.

Unique among spiders, salticids are known to respond to their mirror images by performing threat displays (Forster 1985; Rovner 1989). By using this feature of salticid biology, intrasexual display tests using can be performed one spider instead of two. In one of these tests, the 'pair' of tests spiders is actually one test spider displaying to its own reflection. By testing spiders in the presence of odour of *J. queenslandicus*, the response to mirror images to test conditional strategies in intrasexual contests can be used.

By testing each individual's displays to its mirror image in the presence and in the absence of olfactory cues, the tests situation is more tightly controlled than in previous tests (Wells 1988; Chapters 2-5). When testing pairs of spiders, we can only measure the level of escalation the losing spider was prepared to commit to, and not the level of escalation of spider that was willing to continue with the conflict that is revealed. Testing using mirrors, however, can be envisioned as providing an opponent that is always willing to escalate to the same level as the test spider.

To test the validity of the mirror experiment, olfactory tests were conducted using the methods previously used in Chapter 5. Pairs of *P. fimbriata* males were tested in the presence and absence of olfactory cues from *J. queenslandicus.* This was compared with tests using a single male *Portia*'s response to its mirror image in the presence and absence of olfactory cues from *Jacksonoides.*

MATERIALS AND METHODS

General

All spiders tested were adults from laboratory cultures established by collecting from tropical rainforests in the vicinity of Cairns, North Queensland, Australia. Standard rearing and maintenance procedures were used in a controlled-environment laboratory. Lights came on at 0800h and went off at 2000h. For more details see Jackson & Hallas (1986). All testing occurred between 0900h and 1500h. Because male-male conflict tests were in basic

respects the same as described elsewhere (Chapter 2), only essential details will be provided plus information about the display behaviour of the two species of test spider, *P. fimbriata* and *J. queenslandicus*. The rationale for ranking levels of intensity reached in male-male interactions was as in Chapter 2 and Wells (1988).

Description of displays and ranking

Only brief descriptions of intrasexual behaviour are given here, but details for both species can be found elsewhere (Jackson 1982c; Jackson & Hallas 1986; Jackson 1988). Rankings are listed from lowest intensity to highest intensity.

1) *Portia fimbriata*.

1. Posturing with legs hunched (rank 1). The first three pairs of legs were brought forward, flexed and held close to the body. Adoption of this posture, which was called the 'hunch display', was usually performed while the two salticids were distant from each other, and was typically the display first adopted when a salticid encountered another conspecific. However, hunch display was not exclusive to early in encounters, but instead tended to be the dominant display throughout the interaction whenever spiders were at least 10 mm apart.
2. Posturing with legs erect (rank 1) while no more than 10 mm from the other male (rank 2). The first pair of legs alone, or more often the first two pairs of legs together, were held out stiffly above the substrate at about 45° to the horizontal and were angled between 45-90° out to the side of the males' body. This display was often used briefly at a distance greater than 10 mm in conjunction with the hunch posture, but at this distance it did not qualify as rank 2. While 10 mm or less, from each other, this posture (called 'erect display') tended to be maintained for prolonged periods, during which time the two spiders usually manoeuvred around each other actively.
3. Embrace (rank 3). The spiders brought the front of their cephalothoraxes together and pushed against each other. As the spiders approached the erect legs of the two spiders displaying overlapped as they got closer. The cephalothoraxes of the two spiders were often raised, with the abdomen tilted down. These displays only lasted 5-10 s.
4. Grapple (rank 4). Embracing spiders grappled by moving their overlapping forelegs forward over the opponents' forelegs and forcefully flexing these legs. This display sometimes pulled off one of the opponent's legs.
5. Fight (rank 5). While embracing one male occasionally pushed the other male over onto its dorsal surface. Usually, the up-ended spider righted itself and ran away. However, a fight occurred if the rival spider walked over the up-ended spider. The pair fought by grappling wildly until one male ran away several seconds later. While fighting, the spiders were venter-to-venter.

Experiment 1: Do olfactory cues from prey cause intrasexual interactions to escalate?

Basic experimental procedure

Encounters between two males were staged in a test arena, a Perspex cage (215 mm long X 110 mm wide X 30 mm high) with a removable glass top and removable Perspex end pieces. The bottom of the arena was opaque and an opaque cardboard divider (25 mm high) bisected the centre of the cage and extended out of a slit in the front face of the arena to the outside. When the divider was in place, the two test spiders could see the top of the cork but not

each other.

The basic set up was modified by shortening the arena to 144 mm long X 110 mm wide X 20 mm high and the addition a stimulus chamber (Fig. 26). Shortening the chamber had the effect of decreasing the time that the test spiders took to find each other. The stimulus chamber consisted of a darkened glass vial (40 mm high and 25mm in diameter). The stimulus was stoppered using a removable, lightweight nylon mesh, held in place using a small rubber band. A hole (10 mm diameter) was drilled in the bottom of the vial and lightweight nylon mesh was glued over the hole. The stimulus chamber was set up in such a way as to allow air to flow freely through the vial and into the test arena. A plastic elbow connected the stimulus chamber to the arena. This elbow was round in cross section and fits the stimulus chamber snugly (25 mm inner diameter/35 mm outer diameter). The elbow was approximately 60 mm high and 60 mm wide when viewed side on. A hole (25 mm) was in the back wall and a plastic tube (25 mm in diameter) was placed in this hole. The tube had fine brass mesh glued over one face and when in place the mesh was flush with the back wall. The tube projected from the back wall of the arena and the end of the plastic elbow that was not connected to the stimulus chamber fitted over the tube, connecting the stimulus chamber to the arena.

Recording, analysis and terminology

Interactions were staged by allowing pairs of individuals of the same sex and species (the "test spiders") to encounter each other in the test arena. Natural variation in size and coloration made the identity of the two individuals in any interaction identifiable.

All experiments followed a paired-comparison design: on one day, the two spiders were tested in the presence of a cue from a potential resource (olfactory cue from the stimulus spider); on the succeeding or preceding day (decided at random), the same pair was tested in the absence of this cue. All tests were conducted between 0900h and 1500h. The spiders were tested only once within a single 24-h period. No spiders were tested more than twice. When an individual spider was tested more than once, it was always paired with a different conspecific.

Details about interactions were verbally recorded on tape (Dictaphone) and later transcribed. Key pieces of information used in data analysis were the number of times the spiders embraced, the distance at which the spiders first displayed to one another and the closest distance the spiders were to each other during the test. For a list of displays likely to occur in an interaction, along with brief descriptions for these displays, see above. The distance between the two spiders refers to the distance from the front of the cephalothorax of one spider to the front of the cephalothorax of the second spider.

Appropriate statistics for pair-wise data were used (McNemar tests for significance of changes & Wilcoxon tests for paired comparisons: Sokal & Rohlf 1995). The P-values given are after Bonferroni adjustments whenever the same data are used for multiple comparisons (Rice 1993).

Experiment 2: Do olfactory cues from prey cause male-male interactions with a mirror to escalate?

Basic experimental procedure

The test arena used in the above was modified until it was 215 mm long X 110 mm wide X 30 mm high (Fig. 39). For these tests, the test cage had a stimulus chamber at one end and a mirror at the other end. During experimental test there was a stimulus spider in the chamber. The chamber was empty during control tests.

Like Experiment 1, a stimulus spider was put into a stimulus chamber first and a test spider was allowed to enter the cage c 60 min later to start the test.

Spiders were taken at random from the laboratory stock to serve as test and stimulus spiders. All tests were carried out using adult spiders. No spider was used in more than one test of a given type, although it might be used

in more than one type of test. No spider was tested more than once in a single day. Each test was carried out between 0900 h and 1800 h.

The test spider was first placed in a transparent plastic tube (10 mm in diameter). Within 5 min, one end of the tube was connected to a hole in the bottom of the cage. The spider was gently coaxed out of the tube and into the arena using a fine, camel hair paintbrush. Once the spider entered the cage, the tube was removed and the hole in the cage was plugged with a cork. All tests lasted 30 min.

Recording, analysis and terminology

A paired test design was used: each spider tested provided data from an experimental and control test. When the salticid displayed for the first time during a test, maximum rank of an interaction, distance and latency were recorded. The distance recorded was twice the distance from the spider's anterio-median eyes to the mirror (i.e., the virtual distance from the spider to its own mirror image). Latency was the time that elapsed between the start of the test and the spiders first display. The test continued for 30 min after the spider displayed for the first time. Also, duration (net time spent displaying) was recorded during this period. The test ended if a salticid did not display within 30 min after the start of the test.

RESULTS

Experiment 1: Do olfactory cues from prey cause male-male interactions to escalate?

When the divider was removed the spiders typically turned towards this movement of the divider as it was removed. The spiders would usually turn back the way they were previously facing unless they saw the other spider. Once one spider had seen the second test spider, interactions would proceed as in previous tests. That is the first spider would approach the second spider, usually displaying with hunched legs interspersed with erected legs display. The second spider would turn towards the first and usually displayed with hunched legs or erected legs display. The interaction would proceed in a step-wise pattern with an escalation to higher ranked behaviours until one ran away.

Olfactory cues from *P. fimbriata*'s preferred prey, *J. queenslandicus*, do not appear to affect male-male conflict in *P. fimbriata*. There was no significant change in the maximum rank of a contest (Fig. 40) (Wilcoxon's signed ranks test, 1 tailed, P=0. 29, N=20), the number of embraces (Fig. 41) (Wilcoxon's signed ranks test, 1 tailed, P=0. 22, N=20), the distance at which the spiders first displayed (Fig. 42) (Wilcoxon's signed ranks test, 1 tailed, P=0. 81, N=20) and the distance the spiders closed to in each contest (Fig. 43) (Wilcoxon's signed ranks test, 1 tailed, P=0. 64, N=20).

Do olfactory cues from prey cause female-female interactions to escalate?

Female *P. fimbriata* reacted in a similar manner to the males by turning towards the divider as it was removed. Contests would also start in a similar fashion to males in the previous experiment with one spider approaching the other spider while displaying hunched legs. However on a few occaisions the first spider would not display and appeared to stalk the second spider. If the second spider did not turn towards the first spider the stalking spider would leap onto the second spider. The two spiders would roll around the floor of the arena briefly until one spider ran away. However, in one instance one spider was filled and eaten by the stalking spider.

While there was no significant change in the presence and absence of *J. queenslandicus* olfactory cues in the level of escalation reached (Fig. 44) (Wilcoxon's signed ranks test, 1 tailed, P=0. 25, N=20), the distance at which the spiders first displayed (Fig. 45) (Wilcoxon's signed ranks test, 1 tailed, P=0. 54, N=20) and the distance the spiders closed to in each contest (Fig. 46) (Wilcoxon's signed ranks test, 1 tailed, P=0. 32, N=20), *P. fimbriata*

females would embrace significantly more during contests where the odour of *J. queenslandicus* was present compared with contests in the absence of these cues (Fig. 47) (Wilcoxon's signed ranks test, 1 tailed, P=0. 04, N=20).

Experiment 2: Do olfactory cues from prey cause intrasexual interactions with a mirror to escalate?

Once the test spider was introduced into the arena it would normally wander slowly around it. Occasionally, the test spider appeared to be agitated by the introduction into the arena and would run wildly around the interior. In these instances the spider was put away and not tested until at least 24 h had passed. If the spider did not react wildly it wandered around the arena until it faced the mirror. Usually the spider did not display to the mirror immediately and waited several seconds after facing towards the mirror. Once the spider started to display towards the mirror (usually with hunched legs) it appeared to treat the encounter as if it were displaying towards a conspecific rather than its only mirror image. The spider would approach the mirror displaying with hunched legs interspersed with erected leg display. However, if the test spider attempted to embrace, the two-dimensional nature of the mirror inhibited this display. When *P. fimbriata* embraces they overlap legs, but this was not possible with a mirror. If the contests did not escalate beyond visual displays before ending the interaction would end with the test spider rapidly decamping. However, if the test spider attempted to embrace then the spider typically ended the contest by wandering slowly away and no longer displaying to the mirror even if faced towards it.

In contrast to tests using pairs of males there was a significant difference in tests comparing *P. fimbriata* males' reaction to its reflection in the presence and absence of cues from a common prey salticid, *J. queenslandicus*. In tests where olfactory cues from *J. queenslandicus* were present the test spider would approach significantly closer compared with tests conducted in the absence of these cues (Fig. 48) (Wilcoxon's signed ranks test, 1 tailed, P=0. 04, N=23). However, there was no difference in the level of escalation (Fig. 49) (Wilcoxon's signed ranks test, 1 tailed, P=0. 35, N=23), the latency of the interactions (Fig. 50) (Wilcoxon's signed ranks test, 1 tailed, P=0. 14, N=23), the distance the spider first displayed to its reflection (Fig. 51) (Wilcoxon's signed ranks test, 1 tailed, P=0. 10, N=23), or the net amount of time spent displaying (Fig. 52) (Wilcoxon's signed ranks test, 1 tailed, P=0. 41, N=23).

DISCUSSION

These results show that both male-male and female-female interactions in *P. fimbriata* are influenced by the presence of odour from *J. queenslandicus*. When *J. queenslandicus* odour is detected, intrasexual conflict escalates. Evidently, the Queensland *P. fimbriata* has a conditional strategy: if the potential presence of *J. queenslandicus* is detected, fight harder. The specificity of this rule seems to imply that for both sexes of the Queensland *P. fimbriata*, prey (and specifically *J. queenslandicus* as prey) has shaped the evolution of the Queensland *Portia*'s intraspecific behaviour. Intraspecific display behaviour appears to be in part an adaptation related to competing for prey in this particular species and population of *Portia*.

During tests in which two males of *P. fimbriata* were in the arena (Chapter 5), there was no discernible difference between results in the control test and in tests with *J. queenslandicus* odour present. Yet, when males were tested using the mirror apparatus (this chapter), there was a significant difference between results in the presence versus in the absence of *J. queenslandicus* odour (i.e., *P. fimbriata* males moved closer during mirror tests when odour from *J. queenslandicus* was present). This is initially puzzling. Both tests appear to be testing the same thing, differing only in the way the opponent is presented differing. However, as Enquist et al (1990) point out, contests like this, where contestants use different displays in a logical sequence to test the fighting ability of an

opponent, the progress of the assessment depends on the co-operation of both individuals. Having an opponent that is always willing to match the level of escalation (i.e., the mirror image will always perform the same display as the spider) may exaggerate any escalation between the two experimental conditions. Another factor that may have been important is how the mirror affected embracing. Embracing requires overlapping of legs, but this was not possible with a mirror image.

P. fimbriata females appear to be especially willing to risk performing more dangerous (higher ranked) behaviour when the potential presence of a *J. queenslandicus* was detected. Higher ranked behaviours (e.g., grappling) may subject the spider to greater danger of being injured by the opponent, will cost energy to perform (see Wells 1988) and subject the spider to increased risk of being taken by a predator, because of lowered attention to the environment (see Brick 1998, 1999). Accepting these risks would be adaptive to *P. fimbriata* females if *J. queenslandicus* were a sufficiently valuable resource.

In jumping spiders, as in spiders generally, males contribute only genetic material to the next generation (Elgar 1998). In contrast, females contribute the energy requirements needed for survival from egg to the first prey-capture strategies (i.e., the second instar spiderling) (Foelix 1996). A consequence is that mating repeatedly tends to be more advantageous for salticid females.

For spider females, fecundity is linked to the amount of prey consumed (Heiling & Herberstein 1999). This should make food a more important resource for female spiders than for male spiders. Findings from this chapter (female-female conflict escalated in the presence of prey) support this hypothesis.

In contrast, there was no evidence that *P. fimbriata* males escalated to more dangerous displays when the odour of *J. queenslandicus* was detected. However, *J. queenslandicus* odour causes *P. fimbriata* males to move closer during intrasexual encounters with a mirror. While moving closer to a conspecific (a cannibalistic, araneophagic predator) is potentially dangerous (and shows that these males are willing to accept this risk when a potential prey item is detected), the findings did not show this escalation to higher levels in the presence of *J. queenslandicus* odour. However, the findings on embracing appear to show that *P. fimbriata* males will accept more risk when in the presence of *J. queenslandicus* odour.

The predatory and courtship strategies of *Portia* overlap, because males may be cannibalised by conspecific females, before or after copulation (Jackson & Pollard 1997). Although there is no evidence that *P. fimbriata* females escalate intrasexual conflict in the presence of a male (previous chapter), it would be interesting to test *P. labiata* and *P. schultzi* females because they are highly cannibalistic and often try to eat conspecific males before or after copulation. This is done by using a prey-specific tactic designed to capture conspecific males (Jackson & Pollard 1997). This prey specific tactic (where the prey is a conspecific male), coupled with the fact that females of P. *labiata* and *P. schultzi* actively court males (Jackson & Pollard 1997), suggests that females of these two species view males as a valuable resource both for reproductive and for dietary needs. Therefore findings from testing these two species might be different from the findings from testing *P. fimbriata.*

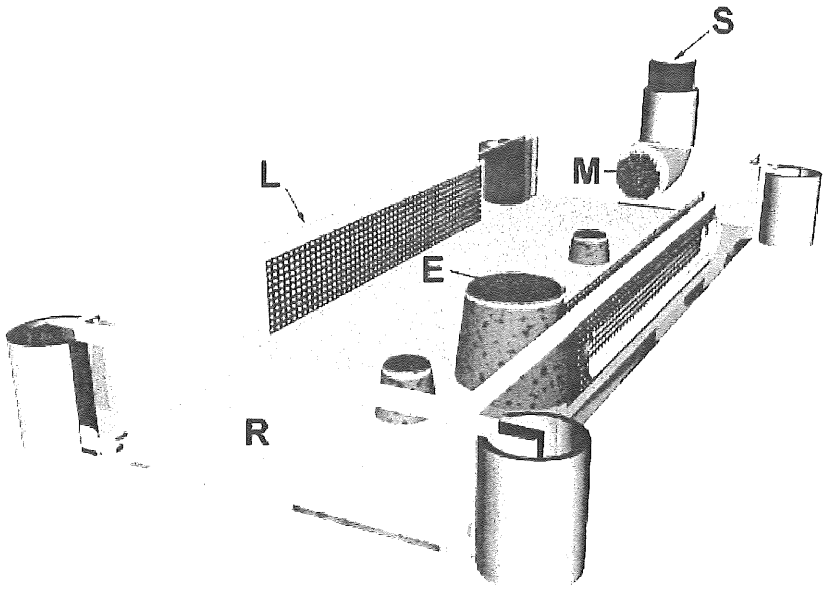

Fig 39: Drawing of transparent Perspex "modular cage" used in mirror tests. E: Hole that allowed entrance for the spider, shown plugged by the cork that prevents the test spider from escaping. L: Glass lid that formed the roof of the arena that allowed observation but prevented the animals from escaping. M: Copper mesh that allowed olfactory cues to enter the arena from the stimulus chamber. R: Mirror, supplying the reflective surface that the test spider displayed to. Shown here as a transparent panel to aid in the visualisation of the arena construction. S: Stimulus chamber, a darkened glass vial containing the stimulus spider that supplied the olfactory cue for the test spider to react to. During the control test the chamber was left empty.

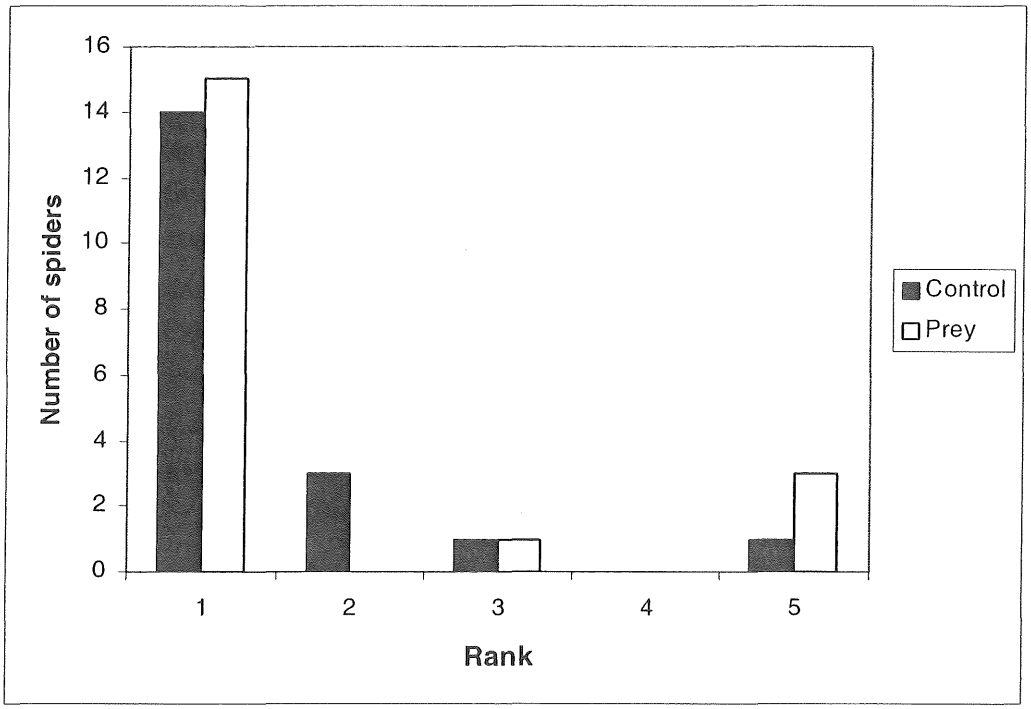

Fig. 40: Number of contests (N=20) of *Portia fimbriata* males at each level of escalation with olfactory cues (from *J. queenslanducus*) present and absent.

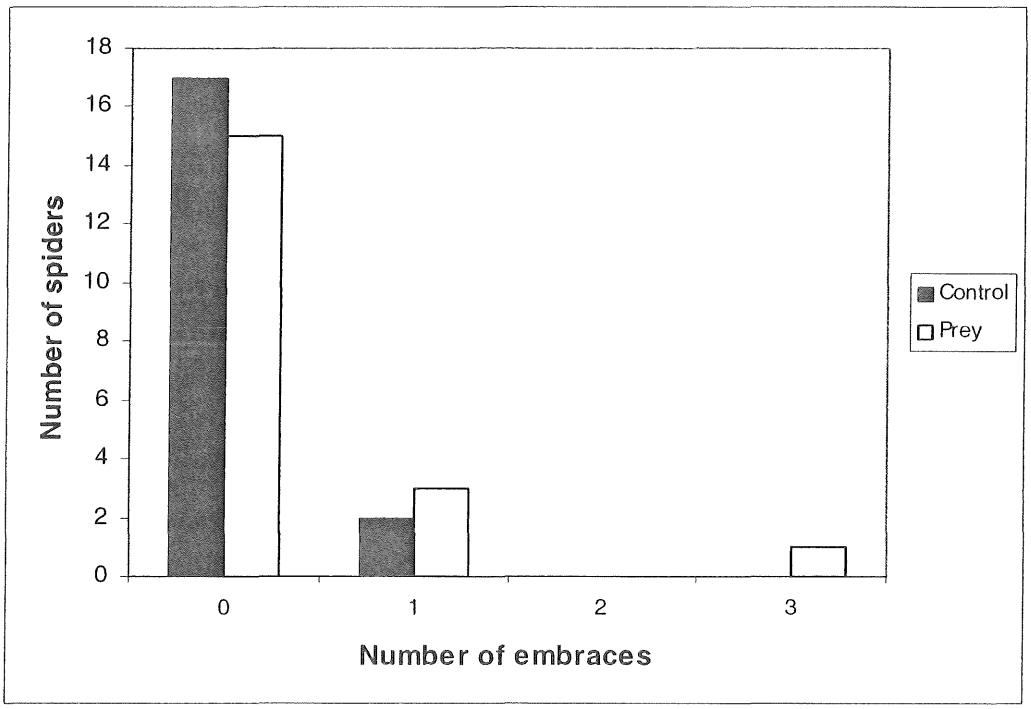

Fig. 41: Number of embraces by *Portia fimbriata* males in each contest (N=20) with olfactory cues (from *J. queenslanducus*) present and absent.

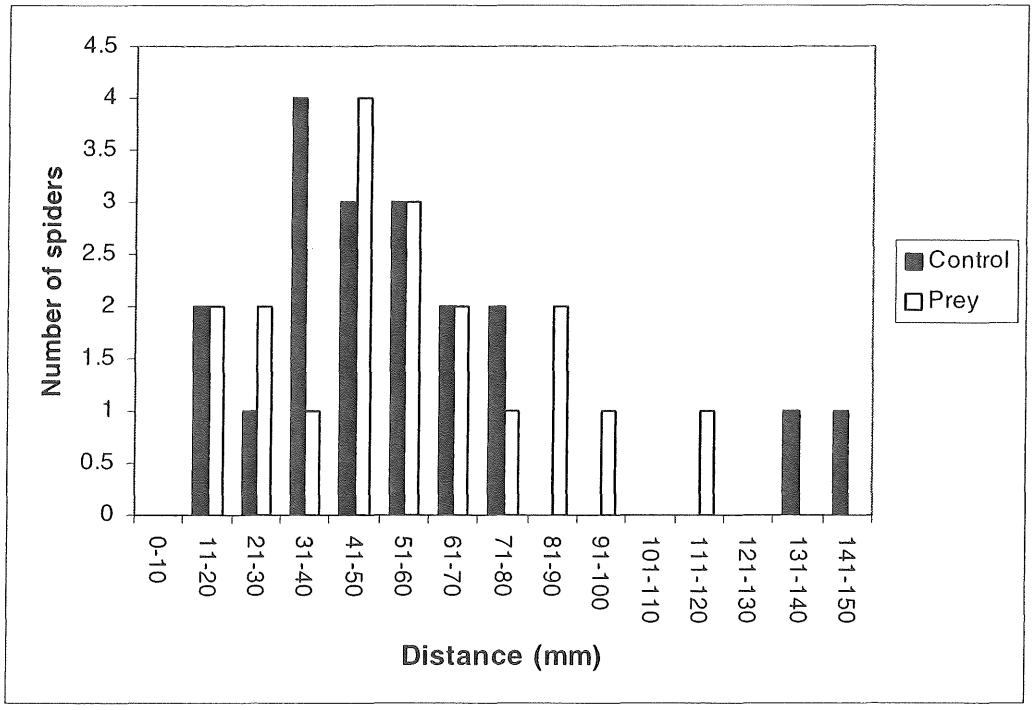

Fig. 42: Comparison of the distance at which pairs of *Portia fimbriata* males first displayed with olfactory cues (from *J. queenslanducus*) present and absent (N=20).

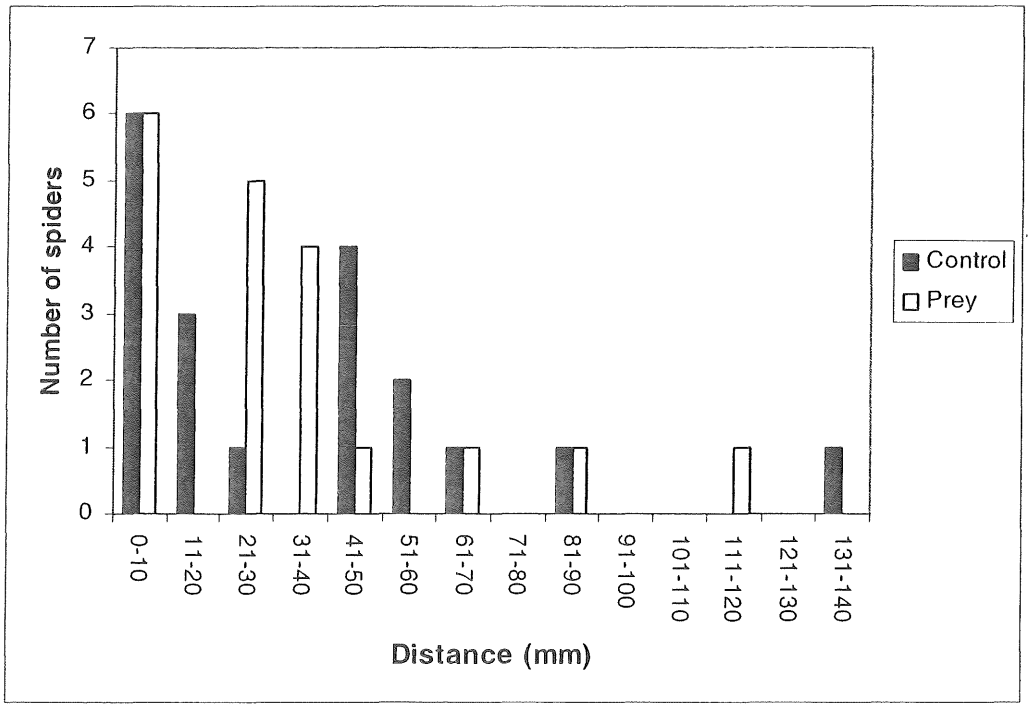

Fig. 43: Comparison of the distance to which pairs of *Portia fimbriata* males closed in tests with olfactory cues (from *J. queenslanducus*) present and absent (N=20).

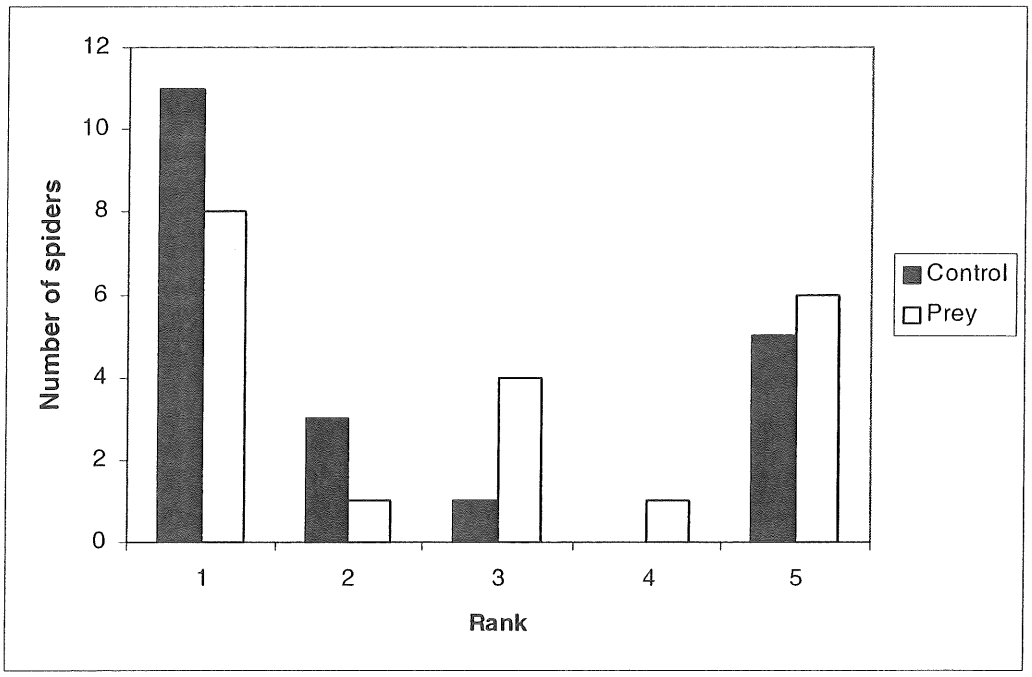

Fig. 44: Number of contests (N=20) of *Portia fimbriata* females at each level of escalation with olfactory cues (from *J. queenslanducus*) present and absent.

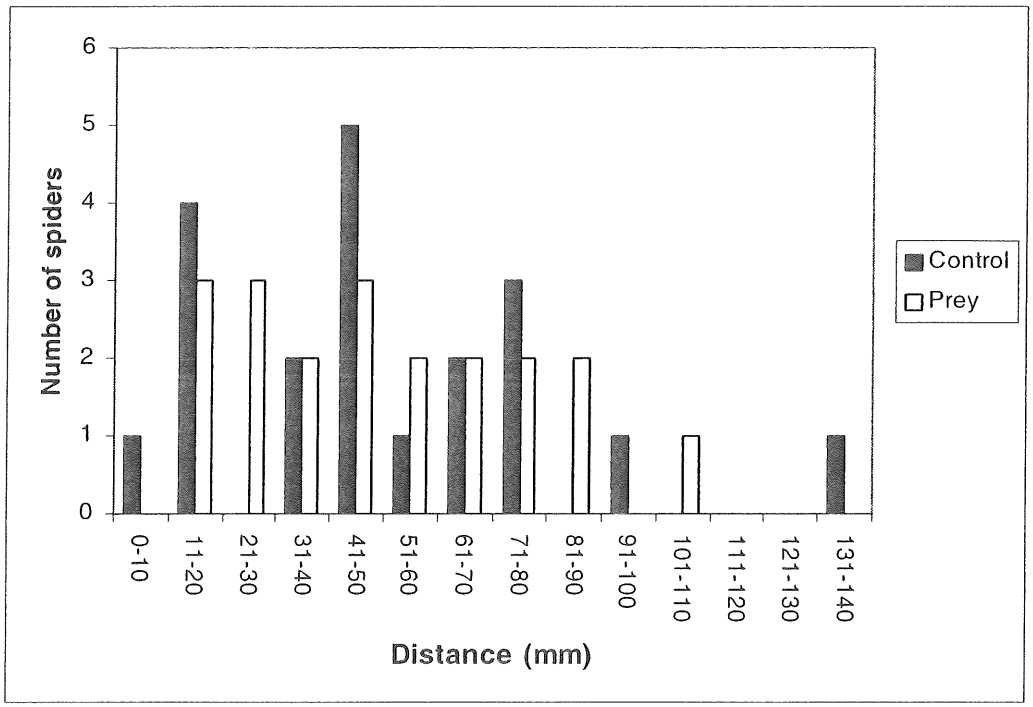

Fig. 45: Comparison of the distance at which pairs of *Portia fimbriata* females first displayed with olfactory cues (from *J. queenslanducus*) present and absent (N=20).

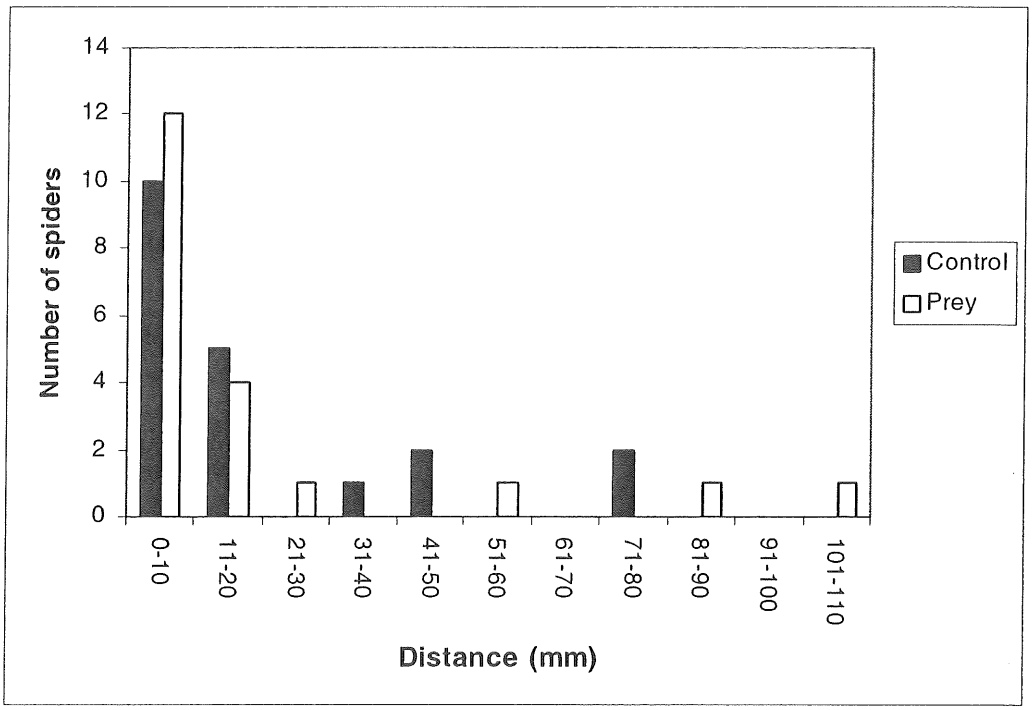

Fig. 46: Comparison of the distance to which pairs of *Portia fimbriata* females closed in tests with olfactory cues (from *J. queenslanducus*) present and absent (N=20).

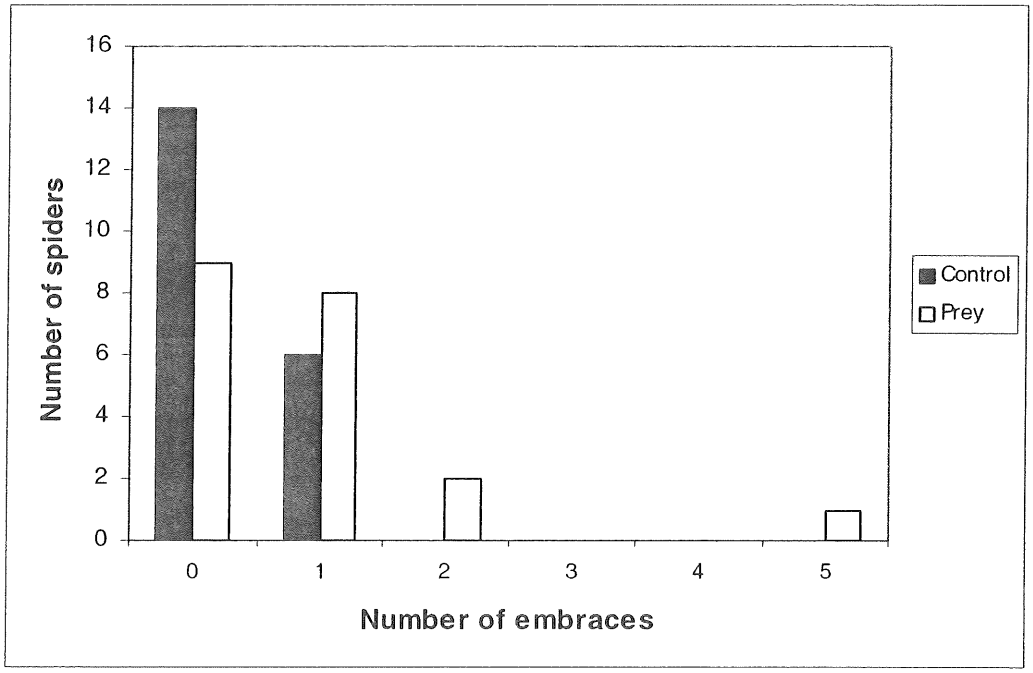

Fig. 47: Number of embraces by *Portia fimbriata* females in each contest (N=20) with olfactory cues (from *J. queenslanducus*) present and absent.

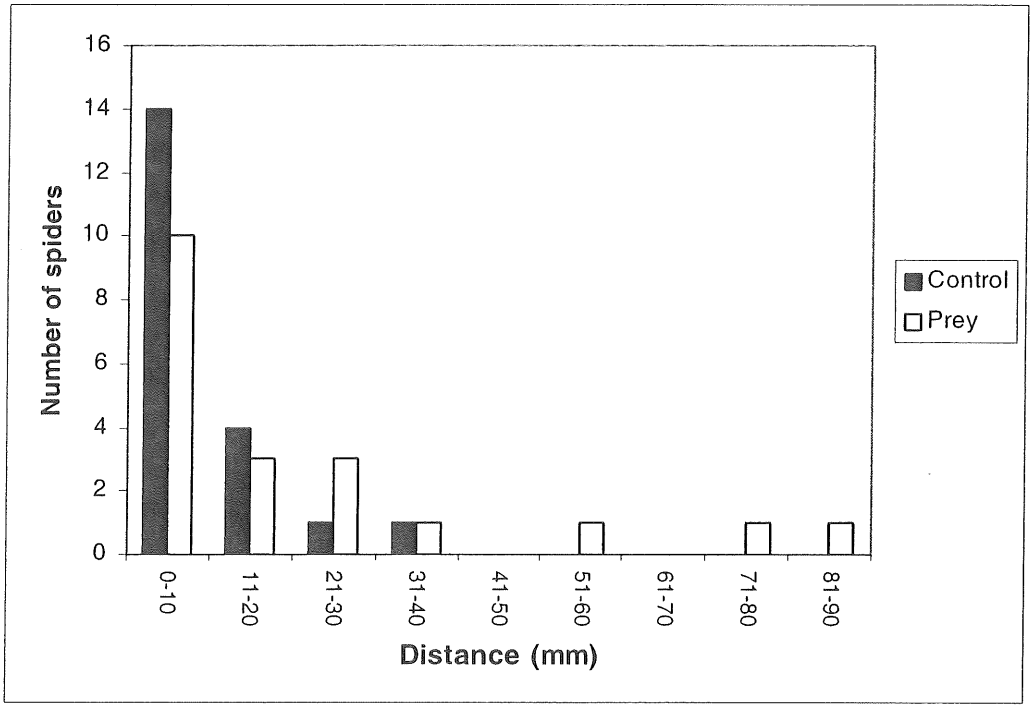

Fig. 48: Comparison of the distance to which a *Portia fimbriata* male closed in mirror tests with lure (made from a conspecific female) present and absent (N=23).

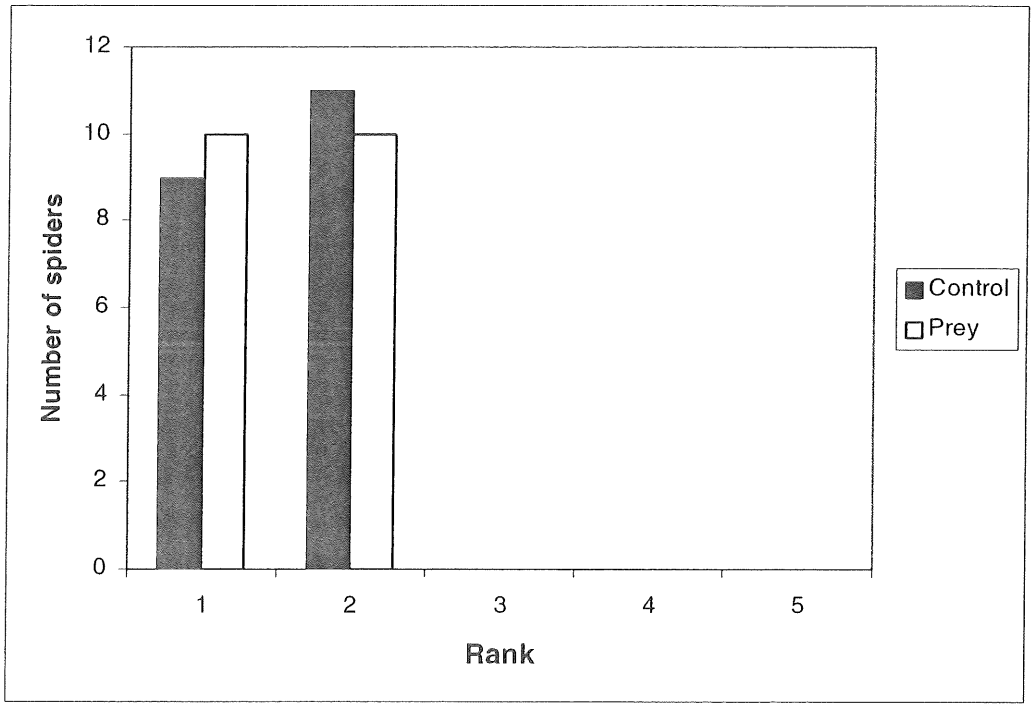

Fig. 49: Number of contests (N=20) of a *Portia fimbriata* male displaying to a mirror image at each level of escalation with olfactory cues (from *J. queenslanducus*) present and absent.

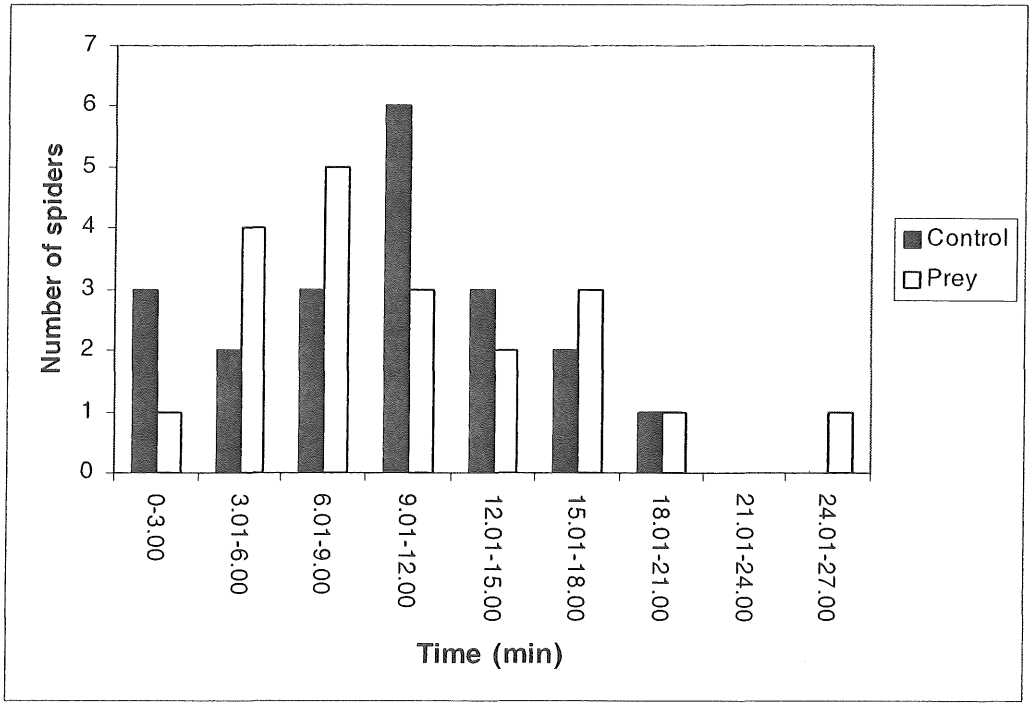

Fig. 50: Latency of contests (N=20) of a *Portia fimbriata* male displaying to a mirror image at each level of escalation with olfactory cues (from *J. queenslanducus*) present and absent.

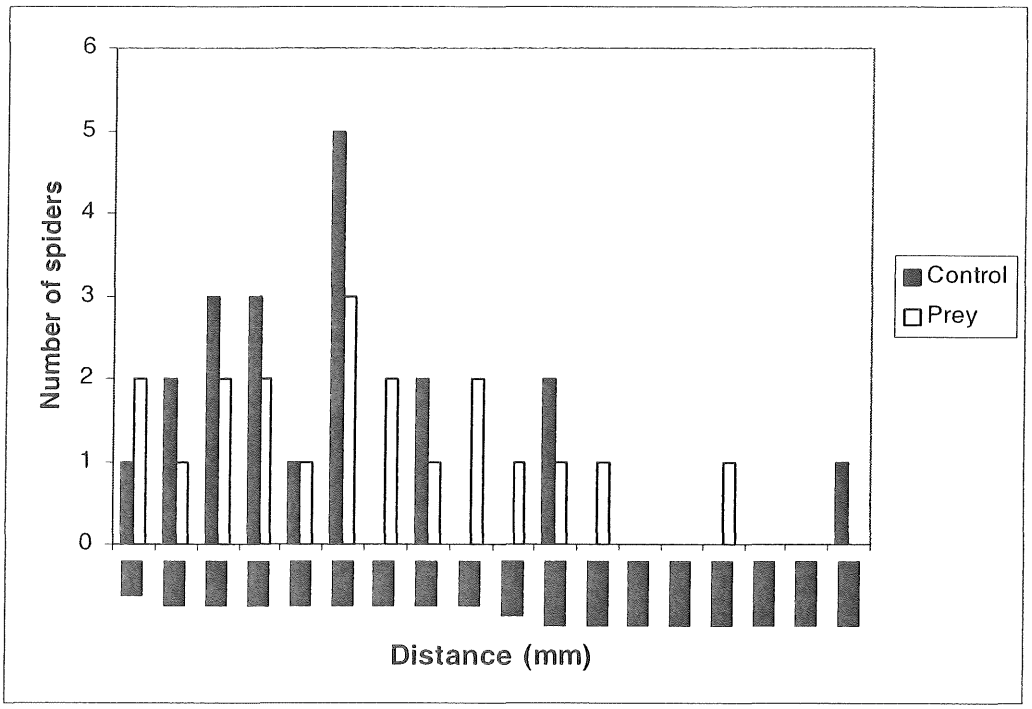

Fig. 51: Comparison of the distance at which a *Portia fimbriata* male first displayed to its reflection in a mirror with olfactory cues (from *J. queenslanducus*) present and absent (N=20).

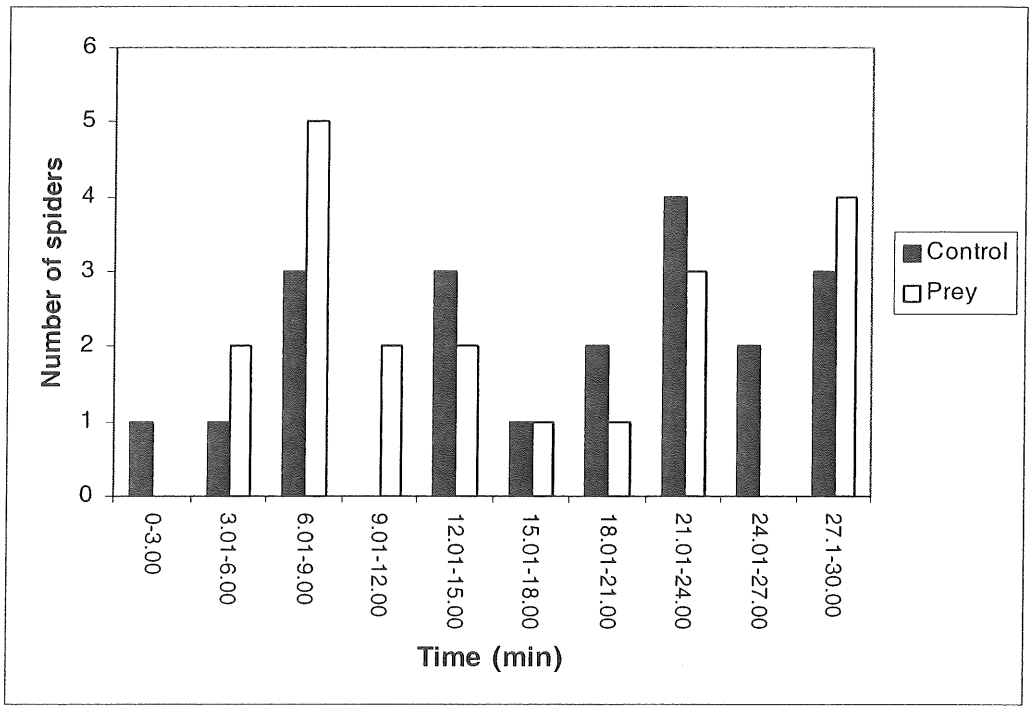

Fig. 52: Comparison of the net time a *Portia fimbriata* male spent displaying to a mirror image with olfactory cues (from *J. queenslanducus*) present and absent (N=20).

Chapter 7: Discussion

CONDITIONAL STRATEGIES

It appears to be appropriate to consider these and Wells' (1988) earlier findings from the perspective of conditional strategies. Conditional strategies are of interest because they potentially reveal specific selection factors that have shaped the evolution of particular behaviour patterns (see Alcock 1998). Studying the rules governing conditional strategies can be envisaged as asking an animal, in experiments, what resources matter to it. In a species with a conditional mating strategy, for instance, each individual has a set of distinct tactics and a set of decision rules specifying the circumstances under which to use each tactic (Dominey 1984): different tactics appear to be adaptively fine tuned to the specified conditions. Conditional mating strategies are widespread, if not universal, in the Salticidae (Jackson 1977, 1982b, 1992a). Wells' (1988) study suggests that salticid males also adopt conditional strategies during intrasexual conflict, but the decisions rules in male-male interaction have not been investigated in depth. These decision rules, once clarified, may help clarify whether the evolution of male-male conflict in salticids has been driven by intrasexual selection.

The first decision rule found in this study can be stated as follows: if movement is detected in the environment (caused by an object the size of a conspecific) escalate male-male conflict. Experiment 1 in Chapter 2 indicates that movement alone, in the absence of other cues, is enough to escalate intrasexual conflict in *E. parvula* males. While the general-agitation effect was not tested in other species, that it was found to exist in *E. parvula* males was enough evidence to incorporate a control for this effect in all visual cue tests. Possibly, the general-agitation-effect acts to heighten awareness in these salticids so that they may be better able to take advantage of a potential resource.

The second decision rule found in this study can be stated as follows: salticid males escalate intrasexual competition in the presence of visual cues from a conspecific female or prey. Although two of the three salticid species studied, *E. parvula* (Chapter 2) and *P. fimbriata* (Chapter 3), escalated the level reached in male-male conflict during lure tests, the third species (*J. queenslandicus*) did not. However, when the male-male interactions of these three species were conducted in the presence and absence of olfactory cues from a conspecific female a different pattern was discovered (Chapter 3). The presence of olfactory cues from a conspecific female causes escalation in two of the three salticid species tested, *J. queenslandicus* and *P. fimbriata,* but not in *E. parvula.*

Interestingly, of the three species studied, *E. parvula* did not appear to detect the presence of a female using olfactory cues. Crane (1949) suggested that reliance on olfactory cues in courtship is a 'primitive' trait and as such more likely to occur in 'primitive' salticids. Work by Jackson and Macnab (1991) also suggest greater reliance on olfactory cues may be the primitive condition. Alternatively, this may be an ecological trend and unrelated to systematics (see Jackson 1982a).

The male-male conflict of Queensland *P. fimbriata* was tested in the presence and absence of olfactory cues of one of the common prey species of this spider, *J. queenslandicus*. While the spiders did not escalate to more dangerous behaviours in the presence of olfactory cues from *J. queenslandicus* the spiders approached closer (Chapter 6). If this finding is common to most salticid species it implies that prey is a resource, but not as important a resource to males as a potential mate. However, more testing needs to be done before this interpretation can be proved.

In contrast to males, salticid females seem to have different decision rules governing intrasexual conflict to males. Females of the three species tested, *E. parvula, P. fimbriata* and *J. queenslandicus*, showed no escalation in

the presence of visual cues from conspecific males (Chapter 4). In contrast to visual prey tests, when the intrasexual conflict behaviour of Queensland *P. fimbriata* females were tested in the presence and absence of olfactory cues, escalation to more higher levels of conflict was detected. Although more tests need to be done this may indicate that prey is a resource to females but conspecific males are not. If this is true then a decision rule for salticid female's intrasexual conflict might be stated: escalate female-female conflict if the presence of a potential prey item is present, but do not escalate if cues from a conspecific male are present.

GAME THEORY

While this study was not testing game theory predictions per se it does support one of the predictions raised by this theory. This prediction deals with resources and can be stated as: the cost a contestant is willing to incur by fighting (contest cost) increases when the value of the resource at stake increases (Maynard Smith & Price 1973; Maynard Smith 1982). In this study the idea that potential mates and prey are a resource for these three species of salticid is tested.

The study mainly concentrated on the idea that adult conspecific females were a resource to male salticids. The three salticid species tested, *E. parvula, P. fimbriata* and *J. queenslandicus*, escalated male-male conflict in the presence of visual and/or olfactory cues from a conspecific female. The escalation detected may be a refined version of the general agitation where the presence of any conspecific immediately prior to intrasexual conflict may escalate that conflict to higher levels of escalation than would have occurred without it. The reaction of male *P. fimbriata* in the presence of prey items, and the female-female conflict behaviour are beginning to suggest that conspecific females are a resource.

Male-male conflict in *P. fimbriata* escalated in the presence of olfactory cues from a prey salticid, *J. queenslandicus*, was compared with tests undertaken in the absence of these cues. Similar results also occurred with *P. fimbriata* females. However, females would escalate conflict to higher ranked displays. Males, in contrast, did not escalate competition to higher ranked displays, but instead approached closer to his opponent (Chapter 6).

In contrast, *P. fimbriata* females did not escalate in the presence of olfactory cues of a conspecific male. While being far from comprehensive these findings suggest that the males are escalating male-male competition in the presence of cues from a conspecific female because the female is a resource rather than being due to the general-agitation effect.

SEXUAL SELECTION

While the main focus of this study is the conditional strategy of male-male conflict in salticids we can begin to interpret the findings in the context of intrasexual selection. From the results of Chapters 2-5 it appears that male-male conflict in salticids may, at least in part, be driven by intrasexual selection. The pattern of escalation in male and female intrasexual conflict in the presence and absence of different potential resources was examined. The pattern that is beginning to emerge strongly suggests that intrasexual selection plays a role in salticid male-male conflict.

Simply put, the pattern that emerged can be stated as: when visual and/or olfactory cues from a conspecific female are present male salticids escalate intrasexual conflict compared with tests in the absence of these cues. Males escalate in the presence of a prey item (see above) but to a lesser extent.

In contrast, the presence of cues from a conspecific male appears to have no influence on female-female conflict. This pattern would suggest that intrasexual selection is acting on the intrasexual conflict behaviour in salticids.

However, that males escalate in the presence of a female is not enough evidence to conclude that males are fighting for females. The possibility that there is some wider effect that causes the escalation measured in male-male conflict still exists. This effect could be envisaged as a refined version of the general-agitation effect but instead of movement causing escalation, it is the presence of, say, a conspecific that causes salticids to escalate. Only by conducting tests that vary the sex of the spider being tested can we definitely conclude that this escalation is due to intrasexual selection.

Also to definitively conclude that intrasexual selection plays a part in the intrasexual conflict behaviour of salticids is to include tests that alter the resource presented to spiders would have to be included. To determine the role of intrasexual selection is beyond the scope of this study, but the pattern of escalation shown in these tests appears consistent with the idea that intrasexual selection forces are at work.

If intrasexual selection was the sole cause of male-male conflict there should be no escalation in the presence of potential resources other than a female. However, escalation was found when prey was used as a potential resource (Chapter 7). From this we can conclude that the prey is a resource to *P. fimbriata* males. However, this means that male-male competition is not solely caused by intrasexual selection.

However, when the results of tests using male *P. fimbriata* intrasexual conflict in the presence of olfactory cues from a conspecific female (Chapter 6) are compared with those tests involving male *P. fimbriata* in the presence and absence of cues from *J. queenslandicus* (Chapter 7) we can conclude that intrasexual selection is the primary driving force compared with the fight for prey. In Chapter 7 male *P. fimbriata* moved closer during conflict if cues from *J. queenslandicus* were present, but there was no increase to more dangerous displays as in all other tests showing escalation. In chapter 6, male *P. fimbriata* were found to be more likely to escalate from visual displays to physical bouts if cue from a conspecific were present. This suggests that prey is less important to males than females. That females are more important than prey to salticid males also matches sexual selection predictions.

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